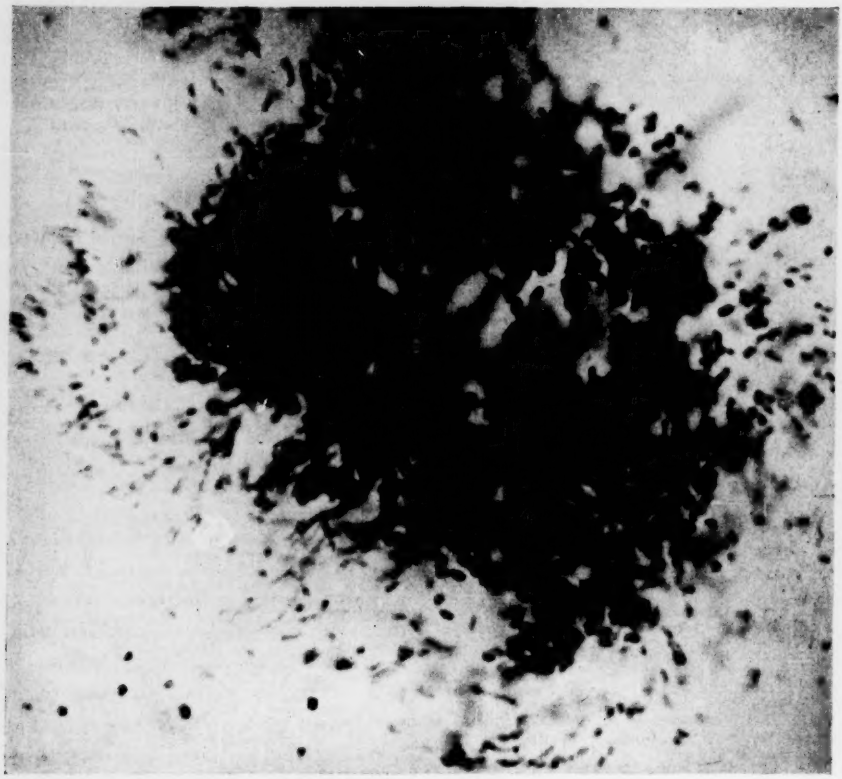
The Journal of HEREDITY



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Haploid Castorbeans

Banded Polytene Chromosomes

Sound-Induced Seizures in Rabbits

Colchicine-Induced Variants in Sorghum

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The JOURNAL OF HEREDITY is published bi-monthly by the AMERICAN GENETIC ASSOCIATION at 32nd Street and Elm Avenue, Baltimore 11, Md., and 1507 M St., N. W., Washington 5, D. C. Address all communications regarding editorial matters to 1507 M St., N. W., Washington, D. C. Communications regarding the business management of THE JOURNAL OF HEREDITY may be addressed to the publication office, 32nd Street and Elm Avenue, Baltimore, Md., or to 1507 M St., N. W., Washington, D. C. Entered as second-class matter February 24, 1923, at the postoffice at Baltimore, Maryland. Acceptance for mailing at the special rate of postage provided for in section 1103, Act of October 3, 1917, authorized December 29, 1918.

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The

Journal of Heredity

Vol. XLV **NOVEMBER-DECEMBER, 1954** **No. 6**

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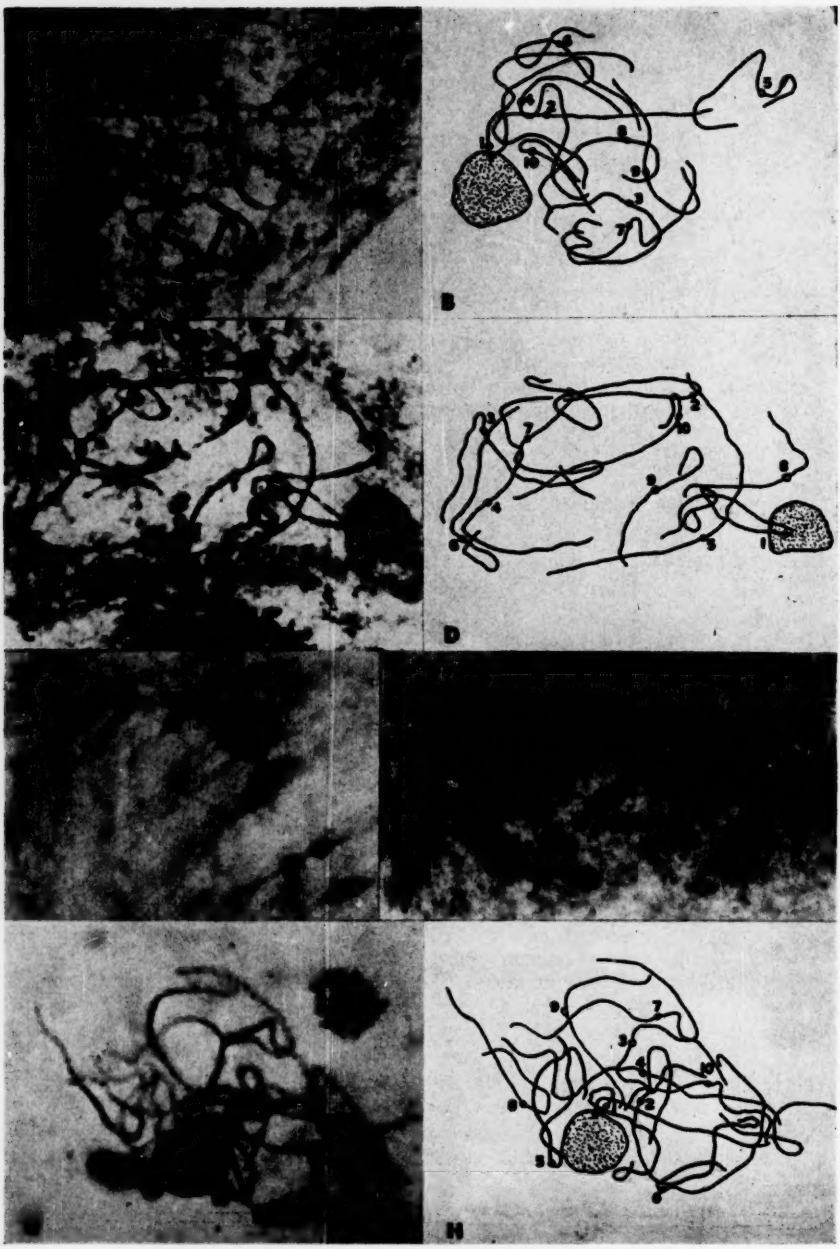

MEIOSIS IN TREATED AND UNTREATED PLANTS

Figure 1

A and *B*—Photograph and drawing of pachytene chromosomes from untreated line 4. *C* and *D*—Photograph and drawing from untreated line 5. *E*—Metaphase chromosomes from untreated line 1. *F*—Diakinesis in an F_1 hybrid between untreated plant 6 and treated plant 15. *G* and *H*—Photograph and drawing of pachytene chromosome from treated line 15.

THE NATURE OF CHROMATIN CHANGES OF COLCHICINE-INDUCED VARIANTS

In Sorghum

D. D. HARPSTEAD, J. G. ROSS AND C. J. FRANZKE*

IN 1948 cytological evidence for the reduction of chromosome numbers in somatic tissue treated with sodium nucleate was observed by Huskins.[3] Other chemicals, including colchicine, were later found to have a similar effect in causing separation of the somatic chromosomes into two or more groups. Evidence for this phenomenon was afforded by the observation of Menzel and Brown[5] who found that one sector of a hexaploid cotton plant contained only half the expected number of chromosomes. They suggested that the origin of this tissue as well as that involved in mosaic phenotypes could be explained by some type of atypical segregational mitosis similar to that described by Huskins.[3] Genetic evidence was presented when Franzke and Ross[2] discovered that true breeding variants with unchanged chromosome number could be induced by colchicine treatment of seedlings of a pure line of sorghum. They proposed that such variant plants could arise through reductional grouping of the somatic chromosome so that a concentration of chromosomes containing gene blocks originating from one of the ancestors might occur in one cell. A cell so formed might either by its genotypical or positional advantage take over the growing point and form a homozygous plant of a different genotype.

Ross, *et al*[8] found that means of measurements made on progenies of variants were outside the range of variability of the original parent variety. In general, the variability within the progenies of the variants was not greater than that of the original. They concluded that gross duplication of chromatin material had not occurred, since no irregularity was noted at the later stages of meiosis. To establish absence of association at earlier prophase a more complete examination of meiosis was necessary. The different phenotypes of the variants might also be due to rearrangements of the chromatin which would be evident in the pairing relationships of these chromosomes with those of the original untreated material. Findings from observations of meiosis in the variants and the untreated full sibs as well as F_1 hybrids between these are reported in this paper.

Material and Methods

Two varieties of *Sorghum vulgare*, Experimental 3 and Experimental 1, were used in this study. Origin of these true breeding varieties has been previously described.[2,8] In addition, six other lines were used as males in crosses with a colchicine-induced variant from Experimental 1.

Fifteen seedlings were grown from selfed seed of Experimental 3. Eight seedlings were selected at random as untreated controls from which were derived lines 1 through 8, while seven seedlings were treated with colchicine as described by Franzke and Ross[2] and gave progeny forming lines 9 through 15. A study of the progenies of these plants has been made by Ross *et al*.[8] Crosses were made between variants and their untreated full sibs as well as among the variants.

From a variety in the breeding nursery, designated Experimental 1, seed of a true breeding variant was re-treated with colchicine. As a result of this treatment, an extreme brachitic dwarf plant originated. Since this plant did not resemble any known ancestral type, it was not considered likely that it had arisen through a concentration of ancestral gene blocks, as had been postulated for

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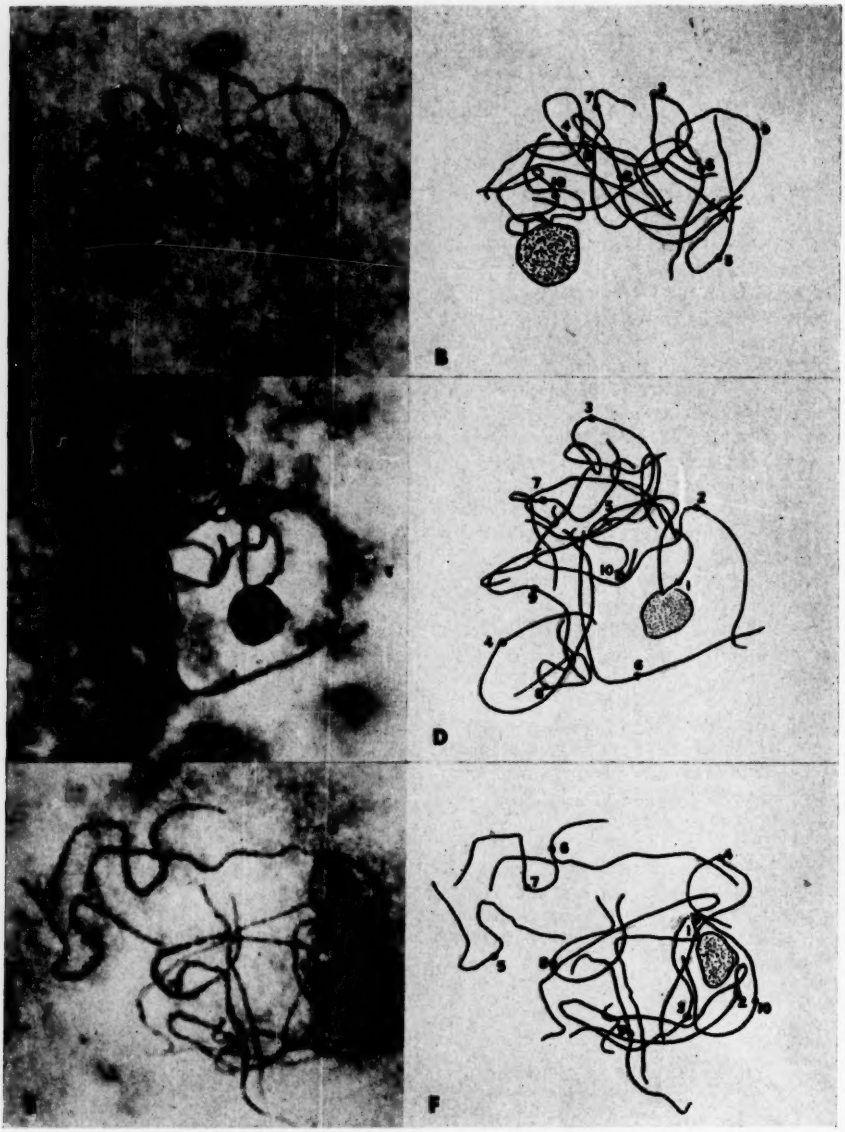

HYBRID PACHYTENE CHROMOSOMES

Figure 2

A and *B*—Pachytene chromosomes from an F_1 hybrid between untreated plant 4 and treated plant 15. *C* and *D*—Pachytene chromosomes from an F_1 hybrid between treated variants 12 and 15. *E* and *F*—Pachytene chromosomes from an F_1 hybrid between dwarf line Ob 31 anl line 80.

variants of Experimental 3. To study the nature of this variant, designated Ob 31, it was used as female in crosses with lines from the breeding nursery designated 20, 30, 40, 50, 60, 70, and 80. Each of these lines had been derived from inbred lines which were treated with colchicine but whose progeny had not expressed gross variations. Line 60 and Ob 31 were derived from treated full sibs.

Material for study of meiosis was fixed in three parts absolute alcohol; one part glacial acetic acid and stored in a refrigerator. Chromosomes were stained with propionocarmine.

Observations and Discussion

To determine the degree of irregularity of meiosis in the untreated plants of Experimental 3, the pachytene stage was examined for the presence of unpaired sections, loops, deficient terminal sections or multiple associations among pairs. In all material, instances of unpaired short sections were observed, but since these were not found in every cell and were not always associated with the same chromosome pair they could not be considered as indicative of lack of homology (Figure 1 *A-D*). The total chromosome complement in 11 cells originating from seven plants, in which the paired homologues were observable along their entire length, was examined and found to have no abnormal pairing relationships. A large number of individual cells were studied in which it was not possible to observe the chromosomes along their entire length. No irregularities were noted in these cells or in cells during later stages of meiosis (Figure 1 *E*).

The behavior of chromosomes during meiosis in seven cells representing five treated variant plants of Experimental 3 was not found to differ from that of the chromosomes in untreated material (Figure 1 *G* and *H*). There appeared to be no changes in frequency of unpaired terminal or internal sections. The complete pairing at pachytene, the absence of multiple association among pairs and the absence of bridges confirmed the findings previously reported.[2, 8]

The pairing relationships of the chromosomes at pachytene in F_1 hybrids between untreated and treated lines were found to be normal (Figure 2 *A* and *B*). Normal pairing was also found when F_1 hybrids between treated lines were observed (Figure 2 *C* and *D*). In studies of the diakinesis, metaphase and anaphase stages no abnormal arrangements were found (Figure 1 *F*).

A similar cytological examination was made of the prophase of meiosis of Ob 31, derived from Experimental 1, the lines involved in crosses with Ob 31 as well as the F_1 hybrids obtained. Complete pairing was observed at pachytene in this material (Figures 2 *E* and *F*). No evidence of association between nonhomologous chromosomes was found. The later stages of meiosis exhibited normal behavior.

As has been previously reported, the base of seedlings of variant lines 12 and 15 was green while the base of seedlings of untreated material was characterized by a deep red color.[8] When crosses were made between untreated lines and either line 12 or 15, the F_1 seedlings exhibited the red coloration. However, when crosses were made between treated lines 12 and 15 all of the seedlings were green, indicating the recessive nature of this inheritance. Reed[7] found that segregation for this character in his breeding nursery occurred in the F_2 generation in the ratio of approximately three red to one green seedling.

The F_1 plants and the parental lines were grown together in a greenhouse soil bed. It was observed that F_1 plants were more vigorous than either of the parents, growing approximately 60-96 inches tall, while the tallest parent was only about 48 inches in height (Figure 3). It must be emphasized that this apparent hybrid vigor resulted when the variant arising through treatment was crossed with its original full sib in the true breeding variety Experimental 3. The F_1 plants exhibited no loss of self fertility. It appeared that the green coloration and apparent hybrid vigor resulted from mutations induced by colchicine treatment.

Very few instances of the possible mutagenic effect of colchicine have been reported. Levan and Ostergren[4] describe variants with unchanged chromosome numbers as dauermodifications. After colchicine treatment of soybeans, Porter and Wiess[6] reported the occurrence of a dwarf strain with unchanged chromosome number. Since Eigsti[1] has shown chromosomal breakages in pollen tubes of *Tradescantia*, it was thought that colchicine-induced variants in sorghum may have arisen through chromatin rearrangement followed by reductional grouping of the chromosomes. However, observations made in this study do not support this hypothesis.

Since several of the variants in Experimental 3 resembled one of the ancestral types, it was thought possible that chromatin may have been duplicated within the chromosome complement, concentrating gene blocks of ancestral origin. The absence in the variants of associations between pairs of chromosomes during prophase of meiosis makes it unlikely that any large sections of chromatin have been duplicated. Other gross rearrangement of the chromatin had not been induced by colchicine treatment since pairing of the pachytene chromosomes was regular in the F_1 plants of crosses between treated and untreated lines. The possibility of the mutagenic effect being

HYBRID VIGOR IN F_1 PLANTS
Figure 3

A—The F_1 plant in the center showing extreme hybrid vigor resulted from a cross between the untreated inbred plant 4 on the left and its full sib, the treated variant 10, on the right. *B*—Hybrid vigor as shown by the center plant resulted when untreated plant 4 and its full sib, treated variant 15, were crossed.

confined to a single gene block or locus is unlikely since many different characteristics have been affected. We are therefore, led to the conclusion that the changes in the chromatin must be of the nature of multiple point mutations perhaps involving minute structural changes which are not detectable through the observation of pairing relationships.

Summary

After colchicine treatment of true breeding sorghum varieties, variants without change in chromosome number arose which immediately bred true. It had previously been proposed that colchicine treatment caused the formation, by reductional grouping of the somatic chromosomes, of a cell with a different genotype which, because of its genotypical or positional advantage, took over the growing point to form a homozygous shoot. To determine if chromatin rearrangement had been responsible for the variant plant type, examinations of meiosis in the original material, in the variants and in the F_1 hybrids between these were made. Analysis of pairing relationships at pachytene in each of these showed that no detectable irregularity or rearrangement of chromatin occurred. The appearance of new phenotypes, and the apparent recessive inheritance of the green coleoptile characteristic lead to the proposal that the colchicine-induced variants have resulted from gene mutation or cryptic structural changes in the chromatin.

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(Received June 28, 1954)

BANDED POLYTENE CHROMOSOMES IN THE OVARIAN NURSE CELLS

Of Adult Diptera

HARRISON D. STALKER*

THE discovery and utilization of the banded polytene chromosomes found in the salivary glands of some dipterous larvae constitutes a tremendous technical advance in the study of theoretical genetics and evolution. While it is true that such chromosomes could hardly have been found in a more useful organism than *Drosophila*, still the presence of equally favorable polytene chromosomes in other groups of flies is not as widespread as might have been wished. Moreover, since the salivary gland chromosomes are generally favorable only in the larvae, this fact limits their usefulness in evolutionary studies to those few forms which can be bred in the laboratory, or (e.g., Chironomous) in which large numbers of larvae may be readily collected in nature. Although banded polytene chromosomes are known to occur in other tissues, such as gut, malpighian tubules and seminal vesicles, and in adults as well as in larvae, still the chromosomes in such tissues are generally so inferior for detailed study, that they are analyzed only with the greatest difficulty. The situation in Rhynchosciara constitutes a marked exception to this generalization.

It has been demonstrated[11] that the banded polytene chromosomes in different tissues show detailed agreeement with respect to their banding pattern. Thus any tissues showing favorable banded chromosomes are of considerable potential usefulness, especially if they occur in the adult, since then organisms which cannot be handled in the laboratory may still be utilized in population studies of cytological variability.

Previous studies in the cytology of the nurse cells of dipteran ovaries in the Muscoid genera *Pollenia, Lucilia* and *Musca* by Bauer[1] and in *Drosophila* by Painter and Reindorp[10] have shown that such cells are characterized by polytene-like chromosomes, but that in the forms studied the banding pattern of such chromosomes is so indistinct as to be worthless for detailed analysis. In *Drosophila* the latter authors have demonstrated a series of endomitotic chromosome duplications leading to the formation of a large number of short, widely dissociated chromosome strands in the mature nurse cell nuclei. In accordance with the multiple strand concept of salivary gland chromosome structure they point out that the principal difference between the chromatid bundles of nurse cells and those of salivary gland cells is that in the latter they are greatly elongated and that there is a close association between homologs. It is the purpose of this paper to describe nurse cell chromosomes in extra-Drosophiline Diptera which in some instances show all of the characteristics of the most favorable salivary gland chromosomes, while at least one case clearly demonstrates the partial dissociation of chromatids characteristic of the endomitotic nurse cells of *Drosophila*.

Materials and Methods

The first species found to show cytologically favorable nurse cell chromosomes was *Lonchoptera dubia* Curran (Family: Lonchopteridae). In the course of examination of acetic-orcein smears of the ovaries of adult flies, well-spread and clearly banded polytene chromosomes were discovered (see Figure 4*A*). It was soon established that these chromosomes were located in the nuclei of the ovarian nurse cells, being most favorable when these cells had reached about one-half of their maximum size.

*Department of Zoology, Washington University, St. Louis, Missouri. These studies were aided by a contract between the Office of Naval Research, Department of the Navy, and Washington University, NR164-108; and by a grant from the National Science Foundation, NSF-C421.

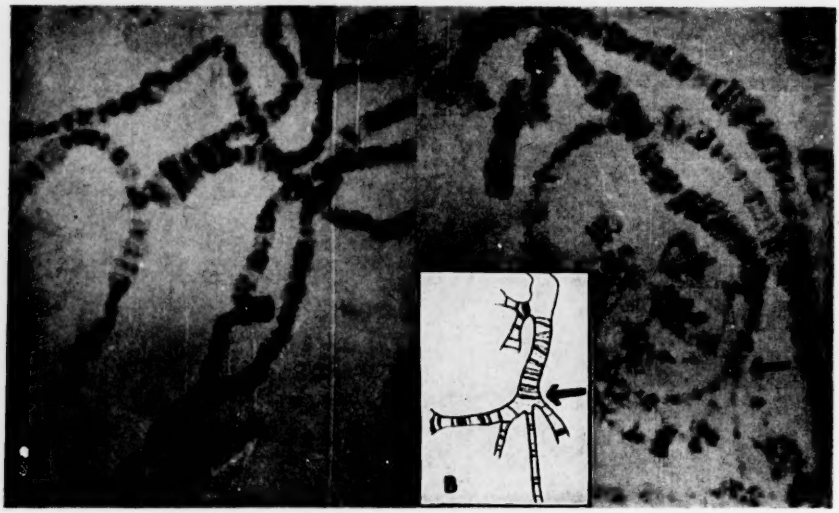
TABLE I. Summary of a survey of ovarian nurse cell chromosomes in various species of Diptera. Only those forms whose names are followed by "positive" or "poor positive" in the last column showed clearly banded polytene chromosomes. All others were negative. Except for some of the species in the family Drosophilidae, nearly all of the data are based on wild-caught flies from the St. Louis area captured from May to October, 1953.

Major Division	*Family*	*Genus and Species*		*Results*
Orthorrhapha Nemocera	Tipulidae		1 sp.	
	Anisopodidae	**Mycetobia*	1 sp.	
	Chironomidae		6 spp.	
	Culicidae		3 spp.	
	Sciaridae	**Sciara*	3 spp.	
	Mycetophilidae		2 spp.	
	Ceratopogonidae		1 sp.	
	Cecidomyidae		4 spp.	1 positive
Brachycera	Tabanidae	*Chrysops*	2 spp.	
	Rhagionidae	*Chrysopilus*	2 spp.	
	Stratiomyidae	*Ptecticus*	1 sp.	
	Bombyliidae	*Sparnopolius*	1 sp.	
	Asilidae	*Atilus*	1 sp.	
	Empidae	*Euthyneura*	1 sp.	
		Platypalpus	1 sp.	
		Drapetis	2 spp.	
		Hemerodromia	1 sp.	positive
	Dolichopidae	*Thinophilus*	1 sp.	
		Laxina	1 sp.	
		Neurigona	1 sp.	
		Asyndetus	1 sp.	
		Paraphyrosylus	1 sp.	
		Sciapus	1 sp.	
		Diaphorus or *Chrysotus*	4 spp.	
		Dolichopus acuminatus Lw.		poor positive
		Dolichopus virga Coq.		poor positive
		Pelastoneurus	1 sp.	poor positive
		Psilopiella	3 spp.	poor positive
		Gymnopternus	1 sp.	poor positive
		Thrypticus	1 sp.	positive
	Lonchopteridae	*Lonchoptera dubia* Curran		positive
Cyclorrhapha Aschiza	Phoridae	§*Aphiochaeta xanthina* Speiser		
		Megaselia	5 spp.	
	Pipunculidae	*Pipunculus*	1 sp.	
	Syrphidae	*Eristalis*	3 spp.	
		Volucella	1 sp.	
		Syrphus	1 sp.	
		Epistrophe	1 sp.	
		Melanostoma	1 sp.	
		Mixogaster	1 sp.	
		Syritta	1 sp.	
Schizophora Acalyptratae	Helomyzidae	*Amoebalaria*	1 sp.	
		Suillia	1 sp.	positive
	Borboridae	*Leptocera*	3 spp.	
	Lonchaeidae	*Lonchaea*	1 sp.	
	Tetanoceratidae	*Melina*	2 spp.	
		Dictya	1 sp.	
		Pteromicra	1 sp.	
		Antichaeta	1 sp.	
	Trupaneidae	*Tephritis*	1 sp.	
	Otitidae	*Rivellia*	1 sp.	
		Euphara	1 sp.	
		†*Chaetopsis fulvifrons* Macq.		
	Micropezidae	*Micropeza*	1 sp.	
	Sepsidae	*Sepsis*	1 sp.	
	Psilidae	*Psila*	1 sp.	
	‡Ephydridae	*Notiphila riparia* Meig.		
		Notiphila pulchrifrons Lw.		
		Hydrellia griseola Fall.		
		Hydrellia formosa Lw.		
		Discocerina lacteipennis Lw.		
		Discocerina obscurella Fall		
		Athyroglossa glaphyropus Lw.		
		Napaea breviceps..breviceps Lw.		
		Nostima scutellaris scutellaris Cress.		
		Typopsilopa atra Lw.		
		Scatella stagnalis Fall.		
		Psilopa atrimana Lw.		
		Psilopa dupla Cress.		
		Paralimna punctipennis Wied.		

*Determination by H. L. Carson.
†Compared with named specimens from A. H. Sturtevant.
‡Determinations by A. H. Sturtevant.
¶Determinations checked and corrected by C. W. Sabrosky.
§Determination by H. Malloch.

TABLE I, Continued

Major Division	*Family*	*Genus and Species*		*Results*
	¶Chloropidae	*Thaumatomyia glabra* Meig.		
		Thaumatomyia pulla Adams		
		Thaumatomyia parviceps Mall.		
		Elachiptera erythropleura Sabr.		
		Madiza latifrons Lw.		
		Madiza trigramma Lw.		
		Oscinella umbrosa Lw.		
		Oscinella neocoxendix Sabr.		
		Oscinella coxendix Fitch.		
		Oscinella soror Macq.		
		Oscinella carbonaria Lw.		
		Oscinella painteri Sabr.		
		Oscinella nudiuscula Lw.		
		Oscinella dorsata Lw.		
		Tricimba spinigera Mall.		
		Diplotoxa versicolor Lw.		
		Eribolus longulus Lw.		
		Melanochaeta eunota Lw.		
		Stenoscinis longipes Lw.		
		Dicraeus wilburi Sabr.		
		Chlorops obscuricornis Lw.		
		Chlorops unicolor Lw.		
		Ectecephala sulcata Sabr.		
		Meromyza americana Fitch.		
		Dorsilopha buscki Coq.		
	Drosophilidae	*Sophophora melanogaster* Meig.		
		Sophophora athabasca Sturt. & Dob.		
		Sophophora bocainensis Pavan & da Cunha		
		Drosophila hydei Sturt.		
		Drosophila immigrans Sturt.		
		Drosophila melanica Sturt.		
		Drosophila nigromelanica Patt. & Wheeler		
		Drosophila robusta Sturt.		
		Drosophila transversa Fall.		
		Drosophila tripunctata Lw.		
		Drosophila macrospina Stalker & Spencer		
		Drosophila putrida Sturt.		
		Drosophila mediostriata Duda		
		Drosophila campestris Burla		
		Drosophila cardini Sturt.		
		Drosophila acutilabella Stalker		
		Drosophila parthenogenetica Stalker		
		Drosophila polymorpha Dob. & Pavan		
		Scaptomyza adusta Lw.		
		Scaptomyza graminum Fall.		
		Chymomyza amoena Lw.		
		Amiota	1 sp.	
	Aulacigastridae	†*Aulacigaster leucopeza* Meig.		
	Agromyzidae	†*Cerodontha dorsalis* Lw.		positive
		†*Liriomyza pusilla* Meig.		positive
		†*Liriomyza melampyga* Lw.		positive
		Phytoliriomyza perpusilla Meig.		positive
		Phytomyza atricornis Meig.		
		Phytobia longipennis Lw.		positive
		Agromyza	1 sp.	
		Phytobia	2 spp.	
		Melanagromyza	2 spp.	
	Chyromyidae	*Chyromya*	1 sp.	
	Chamaemyiidae	†*Chamaemyia polystigma* Meig.		
		¶*Pseudodinia polita* Mall.		
	Anthomyzidae	†*Mumetopia occipitalis* Mel.		
	Lauxaniidae	*Pseudogriphoneura*	1 sp.	
		Homoneura	2 spp.	
		Camptoprosopella	1 sp.	
Calyptratae	Muscidae	*Limosia*	2 spp.	
		Chaetosa	1 sp.	
		Schoenomyza	1 sp.	
		Pseudacicephala	2 spp.	
		Eugenacephala	1 sp.	
		Pyrellia	1 sp.	
		Helina	1 sp.	
		Pseudolimnophora	1 sp.	
		Lispocephala	1 sp.	
		Pselaphephila	1 sp.	
		Fucellia	1 sp.	
	Metopiidae	*Sarcophaga*	2 spp.	
		Helicobia	1 sp.	
		Lucilia	1 sp.	
		Pollenia	1 sp.	
	Tachinidae	*Belvosia*	1 sp.	
		Aphria	1 sp.	
		Megaprotopus	1 sp.	
		Pseudochaeta	1 sp.	
		Microsillus	1 sp.	poor positive



BANDED POLYTENE CHROMOSOMES

Figure 4

A—Banded polytene chromosomes from ovarian nurse cells of *Lonchoptera dubia* Curran. Note the incomplete pairing of homologs. *B*—Banded polytene chromosomes from ovarian nurse cells of *Cerodontha dorsalis* Loew. The arrow shows the region of clearly multiple chromosome strands. The insert drawing indicates some of the details of this region.

The polytene nurse cell chromosomes show the characteristics normally associated with salivary gland chromosomes, including in some instances incomplete pairing or formation of inversion loops between dissimilar homologs. In *L. dubia* there is characteristically very poor pairing of homologs, and in some individuals or cells, none at all. However, pretreatment of the adults with cold appears to improve the pairing considerably. *L. dubia* shows a number of inversions and other rearrangements, and wild populations of this species are being intensively investigated at present.

In addition to the Lonchopteridae, a number of other commonly-occurring Diptera were examined for the presence of banded nurse cell chromosomes, and one of these, *Cerodontha dorsalis* Loew, (Family: Agromyzidae), is of special interest. In an analysis of 117 wild-caught females from the St. Louis area, with the exception of one specimen, all showed good pairing of homologs and homozygosity for the banding pattern. However, an interesting feature of *Cerodontha* chromosomes, rarely found up to this time in other forms, is the fact that the chromosomes do not regularly appear in pairs, as is the case in the salivary gland chromosomes of *Drosophila*, but may occur as 2, 3, 4, 5 or even 6 strands. The distinctness of these strands is especially clearly shown in the heterochromatic regions, (see Figure 4*B*). This multiplicity of strands might at first sight suggest a polyploid species or race. In order to investigate this point further, adults of *C. dorsalis* from the St. Louis area were held in lamp chimneys over flower pots with growing *Panicum capillare* (Panic Grass), according to the method suggested by Luginbill and Urbahns.[6] A number of eggs were laid on the *Panicum* leaves and a larval brain smear was obtained which clearly showed the metaphase chromosomes. In addition to the neuroblast metaphase plates, good figures were obtained in the oogonial cells of two adult females. The neuroblast and oogonial cells show close agreement in their chromosomes, both having three pairs of apparently V-shaped chromosomes, one pair larger than the other two, the latter two pairs having approximately the same length. Since the metaphase chromosomes show the somatic pairing characteristic of the Diptera, and since one of the three pairs is readily distinguished by its size, there is little difficulty in determining that at least in these two types of tissue, the chromosome complement is diploid rather than polyploid. In both oogonial and neuroblast cells the three pairs of chromosomes generally show one arm deeply stained, the other much lighter. Apparently the lightly stained arm is heterochromatic in each case, and thus would not be especially noticeable in the nurse cell nuclei.

In the banded polytene chromosomes of the

nurse cells there are four long euchromatic arms, A, B, C and D. A single well-defined chromocenter, such as that found in some *Drosophila* salivary gland cells is not present, although the four long arms are often connected by heterochromatin, the association nearly always being A-B and C-D. In addition to the long arms some nurse cells show a shorter euchromatic region imbedded in heterochromatin; this may be present in all cells, but it is difficult to study and its invariable presence has not been established. At present the mitotic and polytene chromosomes cannot be homologized with each other, especially so since the centromere regions of the polytene chromosomes are not known.

In spite of the absence of exact information regarding the relationship between mitotic and polytene chromosomes, the clearly diploid condition of the former in the two tissues studied may be considered as evidence that the multiple strands observed in the nurse cell chromosomes are not evidence of polyploidy for the species, but rather indicate secondary dissociation *within* each of the homologous polytene chromosomes.

Preliminary studies of specimens of *Cerodontha* from Pasadena, California, generously supplied by Dr. A. H. Sturtevant, indicate that there are numerous differences in banding pattern between the forms from the St. Louis and Pasadena areas. This difference is being studied further.

Survey of Ovarian Nurse Cell Chromosomes in Other Diptera

With the discovery of banded polytene chromosomes in the nurse cells of *Lonchoptera* and *Cerodontha* a cytological survey of ovaries of other Diptera was initiated. For this survey wild females were collected, principally from the St. Louis area, and their ovaries were dissected in ringer and smeared in acetic orcein. Each specimen was dissected with as little damage as possible, and after the removal of the ovaries was pinned in the usual entomological fashion for later taxonomic identification.

It soon became clear that it was not always possible to classify a given specimen as possessing, or failing to possess, banded polytene chromosomes, since in some cases the only elongated nurse cell chromosomes found had only a faint suggestion of a banding pattern. This uncertainty introduced some error into the survey. As a general procedure all species in which banded polytene chromosomes were doubtfully present were classified as negative. The classification "poor positive" indicated that the banded polytene chromosomes were clearly present, but were (at least in the specimens observed) quite unsatisfactory for cytological analysis. The classification "positive" indicated that the banded chromosomes found appeared to be cytologically workable material. Thus, the error introduced into the classification is one which would perhaps overemphasize the frequency of negative cases. In those instances in which the ovary of the wild female failed to show nurse cells of various sizes, either because of immaturity or because of completed ovarian development, the smear was not considered as evidence for absence of banded chromosomes.

Of course any survey of this type is useful and informative only insofar as both the cytological interpretations and the taxonomic identifications are correct. It is for this reason that the procedures used for identification are treated in some detail. The author has for some years worked in the taxonomy of the family Drosophilidae, and is well acquainted with the local species; he has also worked in a rather perfunctory way in the taxonomy of many other families of Diptera, especially in the Acalyptratae, and is well aware of the pitfalls to be encountered in attempting to identify members of an unfamiliar group by means of keys or descriptive material alone. Thus, wherever possible and practical, the services of specialists were utilized.* In the majority of families, many of them represented by relatively few species, determinations were based on Curran.[3] The use of this work generally permits identification only to genus, and thus for many specimens identification was carried only to this level. In six of the eight families of the Nemocera, the minute somewhat damaged specimens were run through Curran's generic keys with so much difficulty and uncertainty that it was felt the listing of generic names would be misleading, and none is given.

In order that other workers may decide for themselves the probable reliability of the determinations references to the taxonomic papers used by the author are included in the bibliography for all specimens (except the members of the Drosophilidae) determined by the author without the aid of specialists. The footnote references in the table indicate identifications by specialists or those made by comparison with named specimens.

It will be seen from Table I that although one or more species showing banded nurse cell chromosomes was found in every major division of the Diptera except the Aschiza,

*The author is especially grateful to Dr. A. H. Sturtevant for his help in this respect. Dr. Sturtevant has been generous not only in making gifts of named specimens, but also in regard to numerous suggestions as to sources of keys and descriptive papers. In addition he has determined all of the specimens of the family Ephydridae used in this survey. For the checking and correction of the identifications in the family Chloropidae the prompt and courteous help of Dr. C. W. Sabrosky is gratefully acknowledged.

the relative frequency of such species was low, at least in the sample studied. Of the 40 families represented in the survey, seven, or about eight percent demonstrated banded chromosomes. Of the 190 species studied, 16 (also about eight percent) were "positive" or "poor positive."

Discussion

It appears from the above study that in the Diptera the presence of cytologically favorable nurse cell chromosomes is random in a phylogenetic sense, and rather infrequent. However, the survey does suggest that in those species of flies which are of some practical or theoretical interest, but which appear to be cytologically "difficult," examination of the nurse cells and other adult tissues would be worthwhile.

Although it is possible that other orders of insects might show similarly favorable nurse cell chromosomes, with the exception of examinations of a few species of Hymenoptera, Heteroptera and Coleoptera, (all of which are negative), the author has made no observations outside of the Diptera.

In the case of *Cerodontha dorsalis*, the interesting secondary splitting (or incomplete association) of the chromatids *within* each of the homologous polytene chromosomes appears to represent a condition intermediate to the almost completely dissociated chromatids in the endomitotic nurse cells of *Drosophila* and the salivary gland chromosomes of that genus. As such it may be considered to support the multiple strand concept of salivary gland chromosome structure.

Summary

A cytological survey of the ovarian nurse cells of 190 species of Diptera belonging to 40 families reveals the presence of banded polytene chromosomes in 16 species belonging to the families Cecidomyidae, Empidae, Dolichopidae, Lonchopteridae, Helomyzidae, Agromyzidae and Tachinidae.

In some species the nurse cell chromosomes show the characteristics of the most favorable salivary gland chromosomes in regard to size, spreading and detail of banding pattern.

In at least one species, *Cerodontha dorsalis*, the banded polytene chromosomes while showing a striking similarity to salivary gland chromosomes as they occur in *Drosophila*, also reveal incomplete association of the chromatids *within* the homologous chromosomes. This suggests a condition intermediate to that found in the endomitotic nurse cells and the salivary glands of *Drosophila*, and as such may be considered to support the multiple strand concept of salivary gland chromosome structure.

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(Received March 12, 1954)

MICROSPOROGENESIS IN SOME COMMERCIAL POTATO VARIETIES

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THE commercial potato, *Solanum tuberosum* L, has the somatic chromosome number of 48 and is a tetraploid since the basic chromosome number for the genus *Solanum* is 12. Few critical cytological studies in varieties of this species have been made, primarily because of the small size of the chromosomes and the lack of suitable techniques for obtaining good preparations. Satisfactory techniques are now available and hence such studies can be undertaken. Cadman,[2] Lass[6] and Swaminathan[11] have described the nature of chromosome pairing at diakinesis and metaphase of the first division of meiosis in microsporocytes of the varieties Flourball (British), Deodara (Swedish) and Cl.B72 (Mr. J. Clark of Ireland) respectively. Similar information is not available for any American commercial variety. The availability of such data will be of help in the interpretation of genetic results and the formulation of our approach to certain breeding problems.

Material and Methods

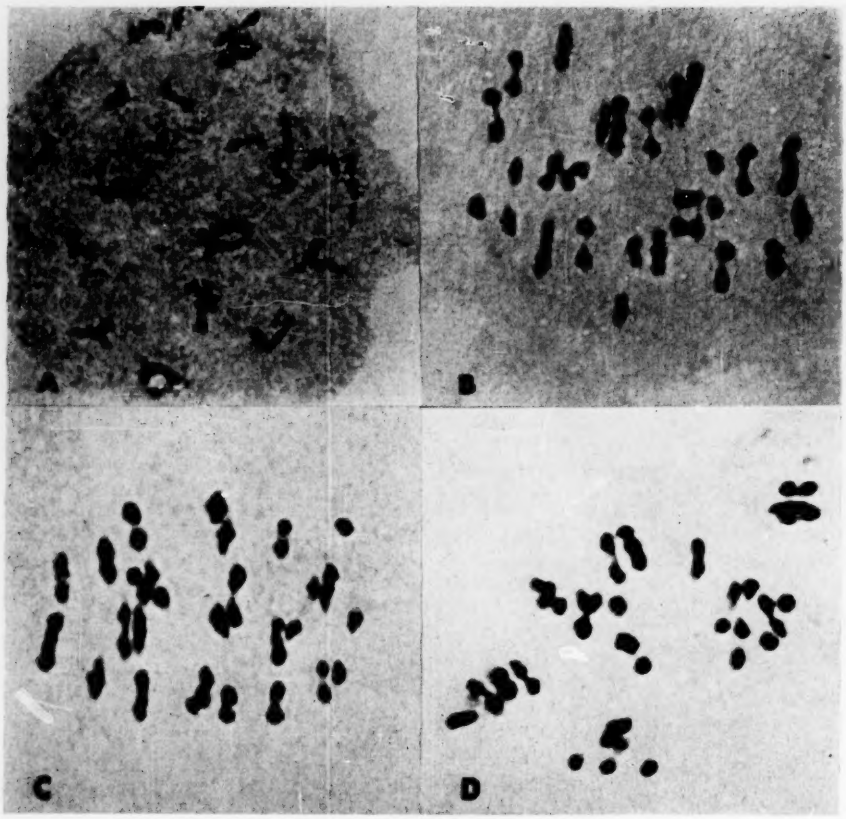
Twelve commercial varieties namely: Chippewa, Cobbler, Earlaine, Green Mountain, Houma, Katahdin, Kennebec, Rural, Sebago and Triumph were used in the present study. The plants were grown in the greenhouses of the Department of Genetics at Madison, at the Branch Experiment Station at Sturgeon Bay, Wisconsin, and in the fields at Sturgeon Bay. In the varieties Chippewa, Katahdin and Sebago, only the chromosome associations at diakinesis and metaphase I were examined.

Anthers containing the desired stages of microsporogenesis were fixed in acetic-alcohol (1 part of a saturated solution of ferric acetate in glacial acetic acid and 3 parts of absolute alcohol) for 24 hours. They were then smeared in drops of aceto-carmine. The schedule described by Marks[7] for preparing aceto-carmine smears gives good results in *Solanum* material. The anthers can be stored in the fixative for several months at 1 to 3° C. As far as possible the fixations were done on the same date and a minimum of three fixations were made in each variety. The analyses were carried out in temporary preparations but a few slides were made permanent for record purposes.

Results

Diakinesis and Metaphase I. A summary of chromosome associations found in these stages is given in Table I. One bivalent was usually attached to the nucleolus at diakinesis. There were, however, several nuclei with two bivalents attached to the nucleolus in the varieties Kennebec and Pontiac. Occasionally, there were two nucleoli in a nucleus in Kennebec with one bivalent attached to each of the nucleoli (Figure 5*A*). A similar occurrence was observed in one instance in Katahdin. The frequency of multivalents in the nuclei examined is given in Table II. Figures 5 *B* to *D* represent metaphase I plates in some of the varieties. Nine quadrivalents were found in a cell at metaphase I in Chippewa (Figure 6), that being the highest number of quadrivalents per cell found in any variety. Among the quadrivalent types encountered, chains and rings of four were the most frequent. A minimum of three chiasmata are required for the formation of a chain of four and a minimum of four chiasmata are required for a ring of four. The quadrivalents, trivalents and bivalents were analyzed for the number of chiasmata present and the chiasma frequency for each variety was determined. The mean chias-

*Paper No. 532 from the Department of Genetics, College of Agriculture, University of Wisconsin. This work has been supported by a grant from the Research Committee of the Graduate School with funds provided by the Wisconsin Alumni Research Foundation. The author is grateful to Drs. D. C. Cooper, G. H. Rieman and R. W. Hougas for advice and help during the course of the study.



DIAKINESIS AND METAPHASE I

Figure 5

All of the illustrations show metaphase I with the exception of *A*. *A*—Kennebec variety at diakinesis. Note the two small nucleoli in the place of the usual single large one. *B*—Katahdin; $2_I + 19_{II} + 2_{IV}$. *C*—Sebago; $1_I + 22_{II} + 1_{III}$. *D*—Red Pontiac; $4_I + 17_{II} + 2_{III} + 1_{IV}$.

ma frequency per cell for the 12 varieties studied ranged from 34.86 in Houma to 38.96 in Chippewa.

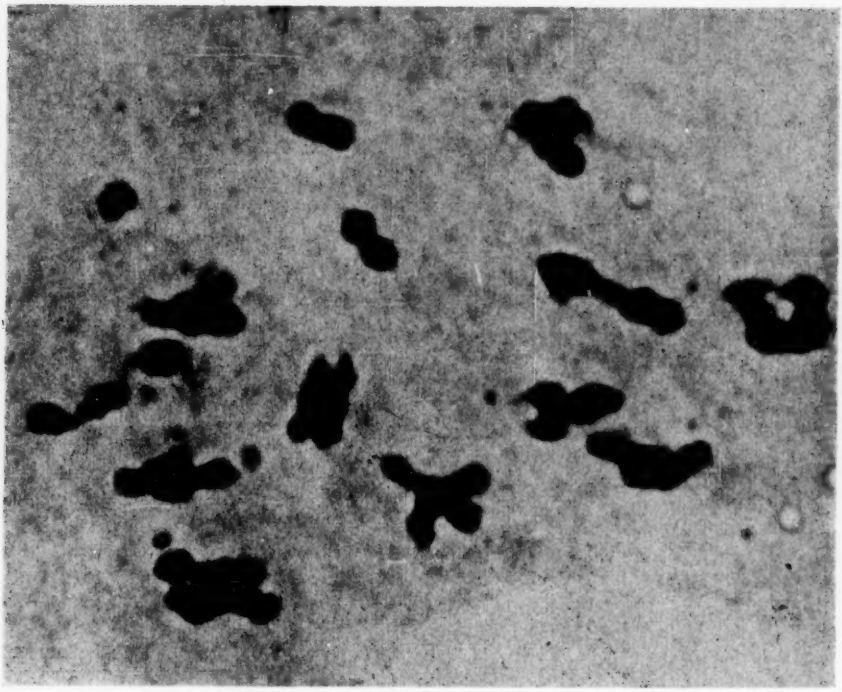
The frequency of multivalents in a colchicine-induced tetraploid plant of *S. polyadenium* (a Mexican diploid species with $2n = 24$) is given in Table II for comparison. *S. polyadenium* has the highest multivalent frequency among the autotetraploids of diploid species studied by the writer.

Both complete and partial failure of chromosome pairing were observed in some microsporocytes of Houma at diakinesis and metaphase I. Two percent of the microsporocytes in Houma and 3 percent of Russet Burbank and Russet Rural showed first division restitution nuclei. The second division may proceed normally in such cells resulting in the formation of dyads of spores or double restitution may take place leading to the formation of monads.

Anaphase I. Anaphase separation was usually regular in most varieties. Dicentric bridges and acentric fragments were observed in 2 to 3 percent of cells in Earlaine, Green Mountain and Russet Rural (Figure 7*B*). Lagging chromosomes which had not gone to either pole were seen in some instances in Cobbler, Houma, Kennebec and Russet Burbank.

Interphase. A single nucleolus was usually observed at each pole but two nucleoli were present at this stage in the varieties Kennebec and Red Pontiac.

Metaphase II. The distribution of chromo-



CHIPPEWA VARIETY AT METAPHASE I

Figure 6

Nine quadrivalents can be seen at metaphase I in the Chippewa variety. Two bivalents are super-imposed over each other, which gives the appearance of a quadrivalent. $2_I + 5_{II} + 9_{IV}$.

somes at metaphase II is given in Table III, (see also Figures 7 *C* and *D*). The distribution in this table should theoretically be symmetrical on either side of the mean, the asymmetry in a few cases being due to the occasional loss of a chromosome from some of the nuclei. Second division restitution occurs frequently in Green Mountain, Houma, Kennebec, Russet Burbank and Russet Rural as a result of the failure of development of a metaphase II spindle (Figure 7 *F*). The percentage of unbalanced gametes given in Table III does not include the cells containing restitution nuclei.

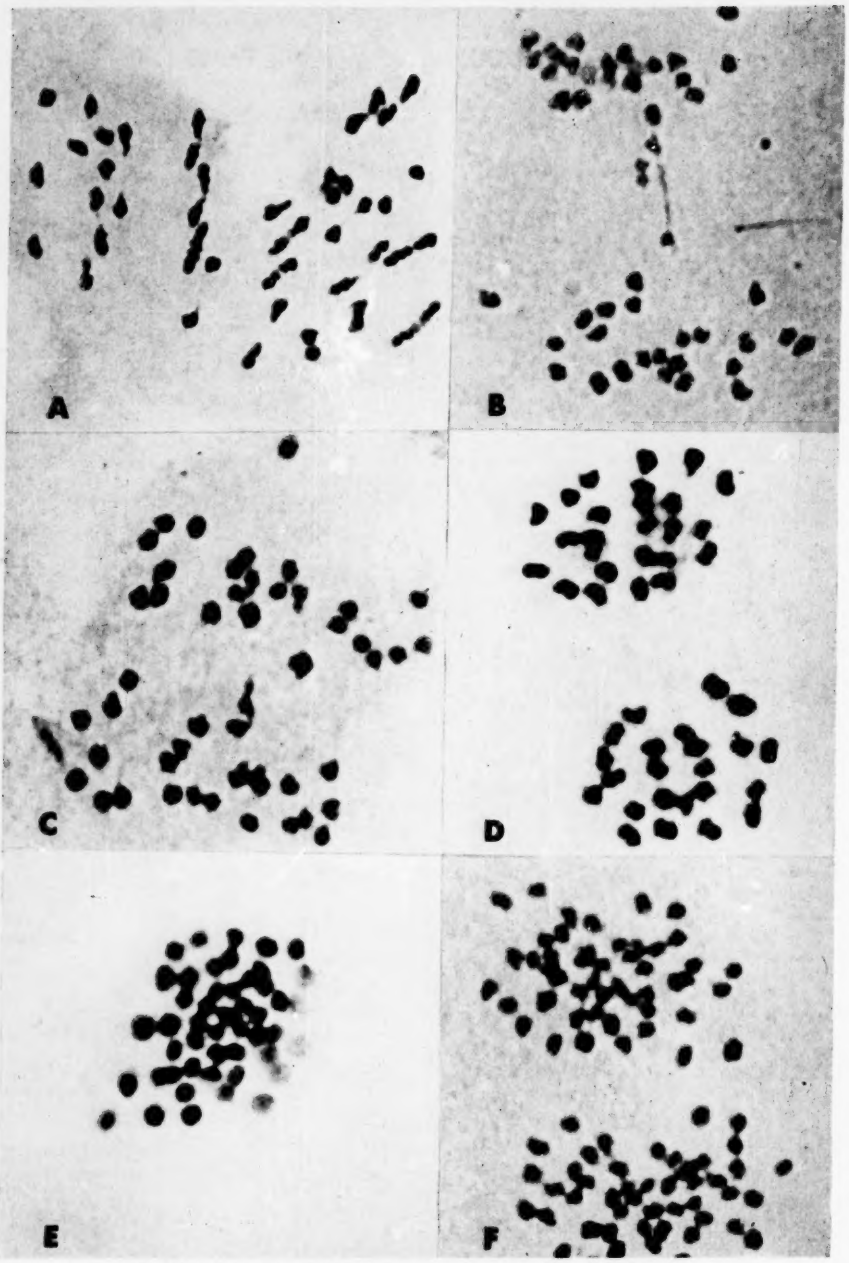
Anaphase and Telophase II. These stages are normal except for occasional lagging chromosomes which may sometimes be grouped together.

Sporads. Tetrads are usually formed following meiosis in the varieties Earlaine, Katahdin and Red Pontiac. A certain proportion of monads, dyads, triads, pentads and micronuclei are also present at the sporad stage in all the other varieties examined. Approximately 30 percent dyads were present in Green Mountain, 35 percent in Russet Rural, 50 percent in Houma and 75 to 80 percent in Russet Burbank (Figure 8 *A*).

Pollen. Pollen samples from the different varieties were stained in aceto-carmine at weekly intervals and the percentage of stainable pollen was calculated (Table IV). The

TABLE I. Chromosome associations at diakinesis and metaphase I in microsporocytes of commercial potato varieties

Variety	No. of cells studied	Mean Frequency Per Cell of			
		Univalents	Bivalents	Trivalents	Quadrivalents
Chippewa	50	1.52	13.84	0.40	4.40
Cobbler	25	1.72	18.20	1.00	1.52
Earlaine	35	1.23	17.20	0.89	2.43
Green Mountain	40	1.25	19.02	0.80	1.57
Houma	14	2.14	17.79	0.86	1.93
Katahdin	50	0.98	18.20	0.58	2.22
Kennebec	50	1.02	20.56	0.46	1.12
Red Pontiac	50	1.34	18.04	0.94	1.94
Russet Burbank	35	1.54	17.69	0.91	2.09
Russet Rural	40	1.00	17.40	0.60	2.60
Sebago	60	2.10	18.08	0.60	1.98
Triumph	15	1.13	16.93	0.60	2.80



ANAPHASE I AND METAPHASE II OF FOUR VARIETIES

Figure 7

A—Kennebec at the beginning of anaphase I. *B*—Green Mountain at anaphase I. Dicentric bridge and acentric fragment can be seen. Also, a univalent is undergoing division at the center of the plate. *C*—Earlaine; metaphase II showing 24 + 24 segregation. *D*—Triumph; metaphase II showing 25 + 23 segregation. *E*—Russet Burbank; first division restitution. *F*—Russet Burbank; second division restitution, which occurs frequently in Green Mountain, Houma, Kennebec, Russet Burbank and Russet Rural as a result of the failure of development of a metaphase II spindle. (× 1450.) .

gaps in the table are due to the fact that the varieties concerned either were not grown in the greenhouse or did not flower in that environment. Earlaine and Katahdin have a high percentage of stainable pollen (Figure 8 *C*), while Houma, Russet Burbank and Russet Rural have practically no good pollen (Figures 8 *B* and *D*). The pollen of Houma is somewhat different from that of the other pollen sterile varieties like Russet Rural in that it takes a certain amount of stain and has an irregular outline due to the lack of an exine (Figure 8 *B*).

Seed Production. Earlaine, Katahdin and Red Pontiac produce seeds on selfing. All the varieties were crossed to Katahdin (pollen parent) and the seed set following such crosses is given in Table V. It is difficult to use Russet Burbank in a breeding program since it is characterized by a high degree of bud and flower abscission. Several methods have been suggested as possible means of stimulating flower and fruit formation in this variety. McLean and Stevenson[8] found that girdling the stem or cutting a stem with the flower axils and growing it in nutrient solutions gives good results. Patterson[9] obtained a satisfactory fruit set after growing the plants between 50 and 60° F. and giving them a day length of 18 hours. Under the weather conditions that were prevalent in July 1953, at Sturgeon Bay (temperature range: 70 to 90° F.) Russet Burbank plants flowered but the flowers tended to drop off two to three days after opening. Berries containing good seeds were obtained following crosses with Katahdin by brushing the pedicels at the articulation points with a 25 mg/litre solution of naphthalene acetic acid prior to and a day after pollination.

Discussion

Most of the present day potato varieties have originated from hybridization among pre-existing varieties. Another species might be involved in a few cases, e.g. Kennebec which has the German "W" race—probably a derivative from *S. demissum-S. tuberosum* hybrids —in its parentage (Akeley *et al.*[1]). It is evident from Table III that a certain proportion of unbalanced gametes occur in all the varieties studied. Also, some varieties form a high percentage of dyads. Nevertheless, all the varieties reported herein as well as those examined by other authors have the somatic chromosome number, $2n = 48$. It would seem that 48 is the optimum chromosome number for *S. tuberosum* and that gametes with chromosome numbers other than 24 are either nonfunctional or are lost during the selection of seedlings by breeders, which may happen if plants with ± 48 chromosomes possess certain economically undesirable characters.

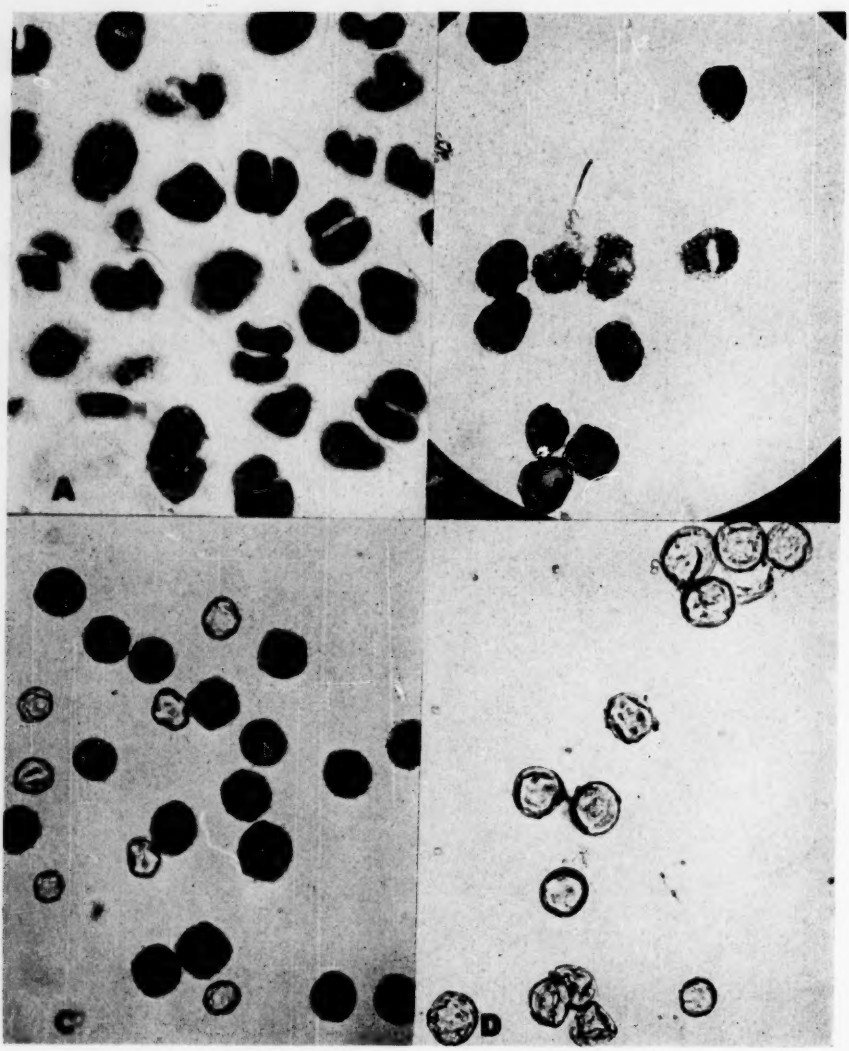
The writer has pointed out elsewhere (Swaminathan[11]) that the results of cytological studies in *S. tuberosum* show that first, 12 bivalents are formed at metaphase I in a haploid plant ($2n = 24$); secondly, a triploid complement forms on an average six triva-

TABLE II. Frequency of multivalents in potato varieties and in an induced autotetraploid

Variety	No. of cells with a quadrivalent + trivalent frequency of											Multivalents	
	0	1	2	3	4	5	6	7	8	9	10	Mean per cell	Coefficient of realization
Chippewa	0	0	3	10	12	8	8	5	3	1	0	4.80	0.40
Cobbler	0	3	7	14	1	0	0	0	0	0	0	2.52	0.21
Earlaine	0	1	7	16	5	4	1	1	0	0	0	3.31	0.28
Green Mountain	0	9	16	7	7	1	0	0	0	0	0	2.38	0.20
Houma	0	0	6	6	1	1	0	0	0	0	0	2.79	0.23
Katahdin	1	6	15	13	11	3	1	0	0	0	0	2.80	0.23
Kennebec	9	11	22	8	0	0	0	0	0	0	0	1.58	0.13
Red Pontiac	1	5	15	15	7	6	1	0	0	0	0	2.88	0.24
Russet Burbank	0	0	15	11	5	2	2	0	0	0	0	3.00	0.25
Russet Rural	0	2	11	12	10	5	0	0	0	0	0	3.20	0.27
Sebago	5	10	12	20	6	6	0	1	0	0	0	2.58	0.22
Triumph	0	2	1	5	4	2	1	0	0	0	0	3.40	0.28
S. polyadenium (4x)	0	0	0	3	4	5	5	4	4	0	0	5.56	0.46

TABLE III. Chromosome numbers at metaphase II

Variety	No. of cells with Chromosome numbers											
	20	21	22	23	24	25	26	27	28	Balanced	Unbalanced	% Balanced
Cobbler	0	1	3	10	90	8	2	2	1	90	27	69.2
Earlaine	0	0	2	9	108	9	2	0	0	108	22	83.1
Green Mountain	0	0	4	6	96	6	4	0	0	96	20	82.8
Houma	0	0	1	6	48	6	0	0	0	48	13	78.7
Kennebec	0	2	1	5	70	3	2	2	0	70	15	82.3
Red Pontiac	0	1	3	7	104	7	3	1	0	104	22	82.5
Russet Burbank	1	2	3	9	68	9	3	1	1	68	29	70.1
Russet Rural	1	0	1	8	38	8	1	0	1	38	20	65.5
Triumph	0	0	2	5	56	5	2	0	0	56	14	80.0



POLLEN GRAINS OF FOUR VARIETIES

Figure 8

A—Russet Burbank. Sporad stage showing monads and dyads. *B*—Houma. Non-functional pollen which will take some stain. Some pollen lack an exine. *C*—Earlaine, showing a good proportion of stainable pollen. *D*—Russet Rural which has no good pollen.

lents; and thirdly a mean frequency of two to three quadrivalents occurs in some commercial varieties. A higher frequency of quadrivalents may be expected in potato varieties on the basis of the pairing behavior in the haploid and triploid. The fact that this is not realized may partly be due to the realization of potential quadrivalents as trivalents and univalents and bivalents and partly to some degree of preferential pairing at the tetraploid level

caused by a slight differentiation of some of the chromosomes. The extent of differentiation may vary in different varieties depending upon the degree of hybridization involved in their evolution. The fact that Kennebec has the lowest quadrivalent frequency among the varieties listed in Table I supports this view. On the other hand, Chippewa, Katahdin and Sebago show significant differences in quadrivalent frequency though theoretically there should be no such difference since Chippewa and Katahdin are selections from the same cross and Sebago is an offspring from a cross between Chippewa and Katahdin. There is not much difference in chiasma frequency among them; hence the observed differences in quadrivalent frequency cannot be attributed to differences in chiasma frequency. It remains to be determined whether this difference between Chippewa and the other two varieties is consistent in different seasons or whether conditions were most favorable for quadrivalent formation in Chippewa at the time of collection and fixation of anthers during the course of the present investigation.

Many of the commercial potato varieties are pollen sterile but readily set seed on being crossed with a variety producing plenty of good pollen. Pollen sterility in the potato has been attributed by various authors to cytological, genetical, physiological and environmental factors acting either singly or in combination. Little is known, however, concerning the stage at which the abortion of pollen takes place in the different pollen sterile varieties. The pollen in Russet Burbank and Russet Rural collapses after the sporad stage and before the first pollen mitosis. Houma has a certain proportion of cells with failure of synapsis during meiosis and also pollen lacking an exine. Preliminary observations on tapetal development in this variety show that mitotic division in the cells of the internal tapetum may be normal or endomitotic. The importance of the tapetum both in the onset of microsporogenesis and the development of the pollen grain has been shown by Cooper,[3] and it is possible that aberrations in tapetal development may be the causation of pollen sterility in many varieties.

Potato breeders and geneticists have long been interested in the question of whether *S. tuberosum* is an auto- or an allo-tetraploid. The writer[11] has discussed this question in detail elsewhere. Stebbins[10] has pointed out the difficulties involved in classifying an existing polyploid plant into one or the other of these two contrasting categories. He has recognized two additional types of polyploids—segmental allopolyploids and autoallopolyploids. It is now realized that an autopolyploid may, soon after its origin, gradually shift to a diploid behavior both genetically and cytologically. The chromosomes of autopolyploid plants may undergo differentiation through structural changes like inversions and interchanges, gene mutation and hybridization, which will lead to a change from multivalent to a bivalent type of synapsis. Gilles and Randolph[4] observed a significantly lower frequency of quadrivalents in an autotetraploid strain of maize at the end of a 10 year period than existed at the beginning of the period. This would imply that one must be cautious when drawing inferences concerning the evolutionary significance of cytological observations made in present-day specimens of a polyploid plant.

A shift to a bivalent type of synapsis will be favored in seed propagated autopolyploid plants both by natural and human selection if there is a reduction in seed fertility as a result of multivalent formation. Human selection will be especially operative if the plant part of economic value is the seed. Such a shift, may, however, be of relatively little importance for purposes of selection in vegetatively propagated plants like the potato. There is also evidence of a negative correlation between pollen and seed fertility and tuber yield in *S. tuberosum* (Krantz[5]). If this is correct, pollen and ovule sterile plants as well as poor and non-flowering ones would have had a selective advantage at least under human selection. Many of the commercial varieties are in fact pollen sterile. Hence, the chromosome associations in current varieties of *S. tuberosum* may be more representative of the situation that existed in this species at the time of its origin than similar associations observed in varieties of a seed-propagated polyploid species. The fact that nine out of a possible 12 quadrivalents occur at metaphase I in Chippewa (Figure 6) and that some potato varie-

TABLE IV. Pollen fertility in potato varieties

Variety	% stainable pollen*								
	Madison, Greenhouse			Sturgeon Bay Greenhouse			Field		
	1	2	3	1	2	3	1	2	3
Cobbler	66	73	69	....	....	....	41	19	38
Earlaine	83	78	81	87	83	85	73	82	80
Green Mountain	....	....	....	18	62	36	10	20	33
Houma	....	....	....	0	1	0	0	2	2
Katahdin	64	77	72	75	58	79	81	73	76
Kennebec	....	....	....	....	....	....	30	48	46
Red Pontiac	....	....	....	35	63	66	59	73	81
Russet Burbank	....	....	....	0	1	0	0	0	5
Russet Rural	....	....	....	4	5	3	0	1	0
Triumph	....	....	....	11	19	21	23	4	29

*Three pollen samples drawn at weekly intervals were studied in each variety under different conditions.

TABLE V. Seed production in potato varieties. (average of 5 berries)

Variety	No. of seeds per berry following self-pollination	No. of seeds per berry following cross pollination — ♀ × Katahdin ♂
Cobbler	0	81
Earlaine	146	153
Green Mountain	0	138
Houma	0	149
Kennebec	0	121
Red Pontiac	103	88
Russet Burbank	0	91
Russet Rural	0	128
Triumph	0	51

ties form nearly as many quadrivalents as a colchicine-induced autotetraploid of a related species would suggest that *S. tuberosum* probably originated as an autotetraploid.

Summary

Microsporogenesis was studied in 12 American commercial potato varieties. All of them were characterized by the formation of trivalents and quadrivalents at diakinesis and metaphase I of meiosis. Nine quadrivalents were observed in a microsporocyte of Chippewa. The maximum number of quadrivalents per cell observed in a colchicine-induced autotetraploid of a diploid species was eight. The varieties studied had several meiotic abnormalities and varying degrees of pollen abortion. All produced seed when Katahdin was used as the pollen parent. It is suggested from the results that *S. tuberosum* originated as an autotetraploid.

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(Received October 30, 1953)

PROCEEDINGS OF THE SEVENTH INTERNATIONAL BOTANICAL CONGRESS

MORE than 1500 botanists from 54 countries met in Stockholm during the summer of 1950 for the Seventh International Botanical Congress. Fifteen years had elapsed since the previous congress at Amsterdam. Consequently, the proceedings of the Seventh Congress* were devoted primarily to the botanical research of the 1940's.

The large number of papers presented at the Congress necessitated publication in abstract form of the papers read at the various sectional meetings. The sectional proceedings, published for the most part in English, include agronomy, cytology, ecology, taxonomy, genetics, morphology, forest botany, nomenclature, paleobotany, phytogeography, phytopathology, physiology, palynology, taxonomy of cryptograms and phanerograms, mycology and bacteriology. Although the individual papers have been condensed, the discussion following the presentation of each paper has been included in the published proceedings. The addresses at the Plenary Meetings and the lectures at the General Meetings have been published in full.

Since most of the papers have been abstracted for publication, it is the reviewer's opinion that this book will be of interest primarily to those who attended the Congress. The details of the various excursions, entertainments and receptions will undoubtedly recall pleasant memories to the botanist present in Stockholm during 1950.

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*Proceedings of the Seventh International Botanical Congress, Stockholm, 1950. Edited by Hugo Osvald and Ewert Aberg. 899 pages, illustrated. Chronica Botanica Company, Waltham, Mass. 1954. $17.35.

IDENTIFYING DISEASE RESISTANCE SUITED TO INTERSPECIFIC TRANSFER

E. E. CLAYTON*

EACH year sees the release of new disease resistant varieties. As has been pointed out by competent observers,[1, 2] many of these varieties achieve little success, and extensive use is still made of old disease susceptible varieties. It is now recognized that some of the old varieties represent an accumulation, over long years of culture and selection, of desirable crop characters, including much disease resistance. In many cases the successful solution of the variety problem requires that the desirable characters of the old varieties be conserved and that needed new resistance be added. Theoretically this is accomplished very easily, merely by repeated backcrossing, using the susceptible variety as the recurrent backcross parent. This is entirely practical when the resistance is inherited simply. However, much of the resistance we are attempting to use is inherited on a polygenic basis. After a cross, repeated selfing and selection is needed to recover the resistance. This delays the speed of backcrossing to the point that the usual release is a varietal compromise; that is a variety which is partly as resistant as the resistant parent and partly as desirable with respect to type, yield and quality as the susceptible parent. In general these compromise varieties have met with limited success.

The most promising solution of this problem appears to be the discovery of better resistance—that is high resistance or immunity which is simply inherited. It is because of this need for better resistance that increased attention is being given to the wild species that are related to cultivated crops. There is a growing literature listing groups of species and their disease resistance. Repeated testing of collections of wild species is necessary since different strains of a species might differ with respect to resistance to disease. However, much of the resistance observed in the wild species is certain to be no better than that already found in cultivated crops. Also, much of the resistance found in wild species will prove to be extremely difficult or impossible to transfer and use, and interspecific transfers are at best slow and costly. So the problem of how to pick the best wild species, on which to concentrate breeding efforts, is very important.

This report is based on work with tobacco and the genus *Nicotiana*—an assemblage of about 60 species. It is of interest to note that this *Nicotiana* group has for a long time proven very useful to students of fundamental plant genetics, and the crop plant, *Nicotiana tabacum*, is basically very similar to many other crop plants. It is an allopolyploid reproduced by seed. The problems involved in interspecific crossings with seed-propagated plants are, of course, different from those encountered with plants that are propagated vegetatively.

These studies have led to a few general conclusions.

1. Valuable disease resistance has not been found in the wild species that are closely related to the cultivated tobacco; that is such species as *sylvestris* and *tomentosa*, which have much chromosome homology with tobacco and which cross readily with tobacco.
2. Highly desirable resistance has been found in some distantly related species that have little chromosome homology with tobacco and which are difficult to cross.
3. It seems likely that the only kinds of disease resistance that would definitely justify the time and expense involved in an interspecific transfer are: (a) monogenic dominant immunity or resistance

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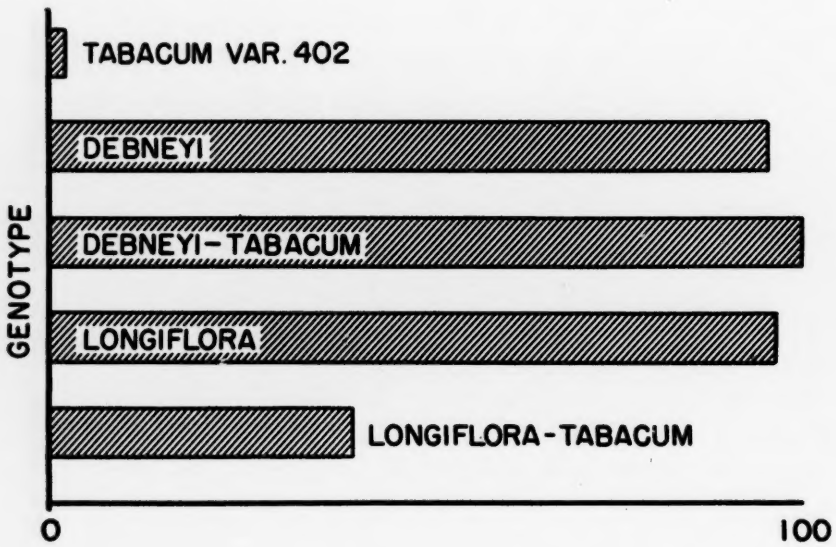

THE RESISTANCE TO BLACK ROOT ROT OF FIVE GENOTYPES

Figure 9

The resistance to black root rot of *Nicotiana tabacum* (var. 402), *N. debneyi*, *N. longiflora*, and the allopolyploid combinations of *debneyi* and *longiflora* with *tabacum*, is illustrated graphically, showing percent root rot resistance. The scale at the bottom represents 0 to 100 percent.

and, (b) possibly high-level polygenic resistance of intermediate dominance, if a major disease is involved, and if adequate resistance cannot be found in the cultivated species.

As to time and expense, it is worthy of note that in the work with tobacco, any interspecific transfer has involved an extensive program, and a minimum of 10 years of continuous work.

Testing for Disease Immunity

If resistance in the form of monogenic dominant immunity exists, it is important to determine this as early as possible. First, because such resistance is most likely to be successfully transferred interspecifically, and second, because once the transfer is accomplished, such resistance will be of maximum value in variety improvement work. Therefore, an important question is—how to proceed most effectively in locating species that have the desirable simply-inherited immunity, providing such species exist? Much effort has been concentrated on the testing and retesting of groups of species. By this process it is possible to eliminate many, and this is most helpful. However, it has not been possible by such testing to distinguish between a species having monogenic dominant immunity and one having high-level polygenic resistance, and yet this distinction is of critical importance.

To take a concrete example: *Nicotiana debneyi* and *Nicotiana longiflora* are both highly resistant to black root rot. Repeated tests have shown no measurable difference in their resistance. Both are difficult to cross with tobacco and the progeny are largely defective and sterile. Because the species are so distantly related to tobacco, and there is little chromosome homology, both species produce stable allopolyploids with tobacco. These polyploid plants grow vigorously and produce normal seed. They have the complete sets of chromosomes from both parents. The behavior of the *debneyi* and *longiflora* black root rot resistance under these conditions is very interesting.

To measure resistance to black root rot quantitatively, duplicate series of plants were grown—one in sterilized soil and the other in black root infested soil. The roots were weighed and the weight obtained in the steri-

IMMUNE ALLOPOLYPLOID

Figure 10

Allopolyploid *debneyi-tabacum*. The left root is from sterilized soil, and the root at the right is from root rot infested soil. The allopolyploid has the same immunity to black root rot as has *Nicotiana debneyi*. This immunity is simply inherited.

lized soil was accepted as 100 percent. The percent resistance in Figure 9 is based on the comparative weight of roots produced in the root rot infested soil. Thus 402, a root rot susceptible tobacco variety, grown in root rot soil produced 1.5 percent of the root weight that was obtained in sterilized soil. *Debneyi, debneyi-tabacum* allopolyploid, and *longiflora* roots grown in the disease-infested soil appeared completely free of black root rot and the root weights, 94.5, 99.3 and 95.3 percent, were all very close to sterilized soil weights. With the allopolyploid *longiflora-tabacum,* however, the root system was severely diseased and the weight of roots produced in infested soil was only 40.6 percent of the weight produced in sterilized soil (Figure 9).

Thus the tests with the allopolyploid revealed a difference that tests with the parent species had not shown. The polyploid test proved that *longiflora* black root rot resistance is not dominant. On the other hand, the test indicated that *debneyi* black root rot resistance is dominant, and it could be one of the simple types of monogenic dominant immunity for which we search.

This same species, *Nicotiana longiflora,* which does not have resistance to black root rot that is suited to interspecific transfer, does have monogenic dominant immunity to wildfire, a bacterial disease affecting tobacco. The *longiflora-tabacum* polyploid shows the wildfire immune reaction, just the same as the *longiflora* parent.

On the other hand, *Nicotiana debneyi* is highly resistant to the blue mold disease of tobacco. The blue mold resistance of the allopolyploid *debneyi-tabacum,* however, is only intermediate and later results have shown it to be polygenic. Work on the transfer of this particular resistance has proceeded despite this unfavorable circumstance, because adequate resistance to blue mold does not exist in *Nicotiana tabacum.*

There are, in the literature, numerous reports dealing with the inter-specific transfer of polygenic resistance, that reacts as an intermediate when tested in F_1 or in the allopolyploid combination with susceptibility. Very little in the way of positive achievement has followed these reports, and in many cases the work has apparently been dropped after one or two generations. The blue mold transfer involves this type of resistance. It began with a cross made in 1937, and the work has been carried far enough now to give a clear picture of the problem of interspecific transfer with polygenic resistance. Suffice it for the present to note that the transfer of this polygenic resistance has already involved time and expense ot a magnitude that would not encourage many such undertakings.

To pass now to a slight variation of the disease indexing method under consideration: When some species of *Nicotiana* are crossed with tobacco, an F_1 results that grows vigorously but is sterile. This F_1 is chromosomally balanced the same as an allopolyploid, with the same kinds of chromosomes but with only half as many, and the plants serve equally well for testing resistance. For example, the *glutinosa-tabacum* F_1 gives the same local lesion necrotic reaction as the parent *glutinosa.* As is well known, this necrotic reaction is another monogenic dominant.

It is obvious that obtaining an immune reaction with either the allopolyploid or the F_1 does not definitely prove how this resistance is inherited. The important point is that when the polyploid or the F_1 gives an immune reaction this is a most favorable indication. If, on the other hand, the polyploid or F_1 gives an intermediate resistance reaction, this is a warning that the resistance being tested is not completely dominant. Frequently such resistance is polygenic.

An illustration is given below of the allopolyploid test in comparison with what might be termed the usual progeny test. Recently Valleau[4] reported that *longiflora* was immune to black shank, that the immune factor was completely dominant in the F_1, and that immune-plants were recovered in the first and second backcrosses. Such results would indicate that *longiflora* has simply inherited immunity to black shank that is probably monogenic. The need for black shank immunity is very great and, if this conclusion were correct, there would be no occasion to look beyond *longiflora.*

During the past several years repeated tests have been made of the *longiflora-tabacum* polyploid resistance to black shank. In the field it has proved highly resistant to the disease, but not as resistant as *longiflora.* In the greenhouse, under controlled conditions, it has been possible to show a marked difference between the resistance of *longiflora* and the resistance of the *longiflora-tabacum* polyploid to black shank. For example, in one carefully conducted test, black shank killed 80 percent of the polyploid plants and less than five percent of the *longiflora* plants. These tests with *longiflora* black shank resistance consequently lead to the conclusion that the resistance is not dominant, and tests with thousands of progeny from the backcross to tobacco indicate that *longiflora* resistance is not inherited on a monogenic basis. More highly resistant strains of *longiflora* may, of course, exist. It is to be noted that with a cross between *longiflora* and tobacco all plants in the F_1 and first backcross generations are very unstable, and hence any plant material tested is not available for retest. On the other hand, the allopolyploid *longiflora-tabacum* is stable and seed is available for retest. It has always been found necessary to make repeated tests before deciding on the resistance level of any genotype, because low resistance may appear very high under conditions unfavorable for disease development.

A final illustration of the possibilities of the procedure suggested: There is an extensive literature on the resistance of *Nicotiana* species to powdery mildew. Among the species repeatedly mentioned are *sylvestris* and *glutinosa*; both are reported as highly resistant or immune. Both *sylvestris* and *glutinosa* produce vigorous growing F_1 plants, when crossed with tobacco. As early as 1934 it was reported[3] that the *tabacum-sylvestris* F_1 was intermediate in resistance to powdery mildew, while the *tabacum-glutinosa* F_1 was immune. This report[3] would indicate that *glutinosa* and not *sylvestris* should be used as a source of powdery mildew resistance. The *sylvestris* cross with tobacco is very easy to make, however, and it is perhaps significant that, so far as is known, stable powdery mildew resistance has not been successfully transferred to tobacco despite continuous work in a number of countries for many years.

Utilization of allopolyploids, or where they are available vigorous growing F_1's, to critically evaluate disease resistance in wild species, has a definite practical advantage. Many of the *Nicotiana* species are small in size and difficult to handle under ordinary field conditions. The combination with *N. tabacum* results in generally larger and more vigorous plants that are much easier to test.

Conclusion

In conclusion—to select a wild species suitable for an interspecific transfer of disease resistance the following is suggested:

1. By repeated evaluations of the disease resistance of available species, narrow the choice to those that are uniformly highly resistant or immune.
2. Measure the disease reaction of these species in direct comparisons with the allopolyploids or F_1's that they form with the crop plant, in this case tobacco.
3. If possible, use for interspecific work a species that produces an allopolyploid or F_1 which shows the full resistance of the resistant parent.

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(Received June 16, 1954)

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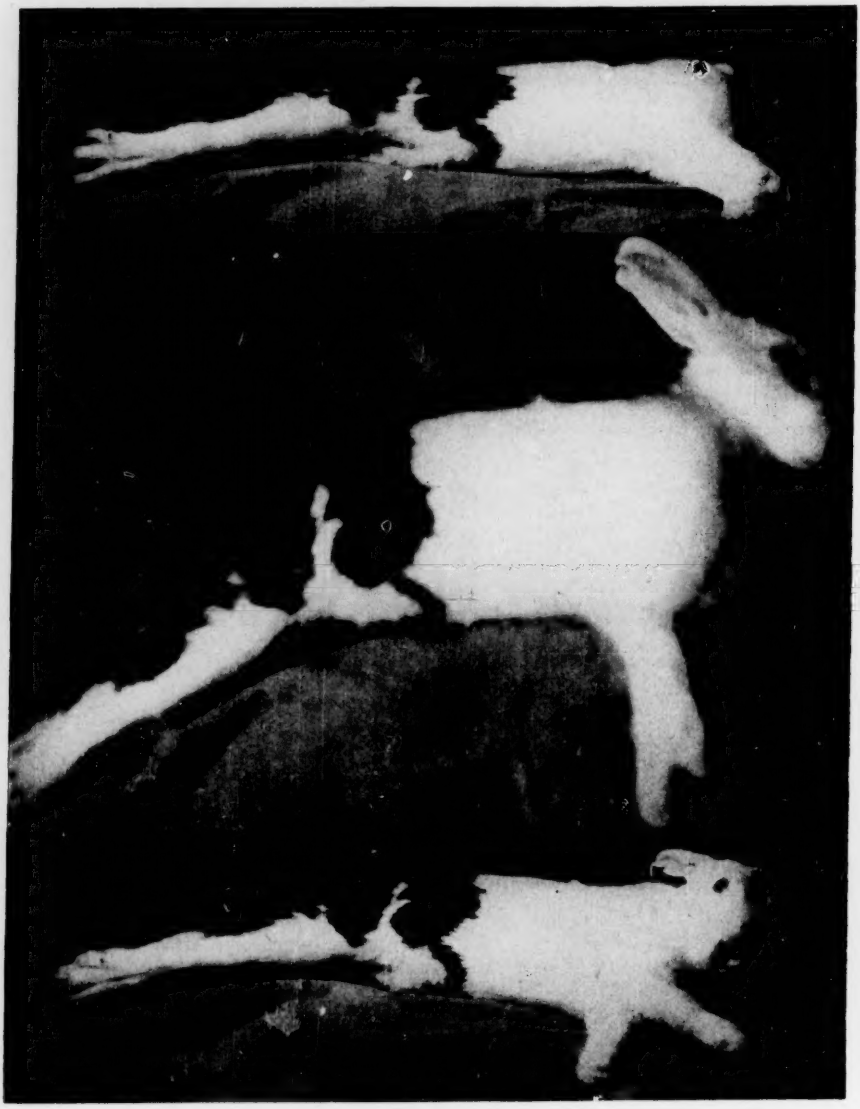
Our Greatest Human Resource: How It Is Wasted

. . . . THE necessity of maintaining a continuous flow of an adequate number of well-trained scientists and engineers results from our country's increasing dependency on technology and technological defense needs, especially in view of Russian's all-out effort to increase their supply of scientists and engineers. . . .

Since 1950 there has been a decline in the number of college graduations. This is due primarily to the low birth rate twenty-two years ago at the depth of the great depression. Fortunately, we are apparently at the expected low point in college graduations, since from now on the increased birth rate after the depression will be reflected in the number of our college graduations. . . . With this increase in our population the task before us in maintaining the quality of training of this great increase in enrollments is one of the most serious problems facing us in maintaining economic and defensive strength.

While estimating supply or demand for manpower in the scientific specialties is always difficult, there is one kind of shortage that is always with us, namely, a shortage of top-flight creative scientists in all fields. I mention this shortage because there is evidence that too large a percentage of our most highly qualified youth drops out of the educational system entirely between high school and college. While the number of creative scientists should increase as college enrollment increases, and while it is possible to increase the supply of such scientists by encouraging those who presently go to college to continue through graduate school and into careers in research, we must not overlook the important group of potentially creative scientists who do not at present even enter college. . . . —Dr. Alan T. Waterman, Director, National Science Foundation, before the Sub-committee on Educational Activities of the Federal Government, of the Committee on Education and Labor, House of Representatives, November 17, 1954.



SOUND-INDUCED SEIZURES

Figure 11

Three successive stages in the convulsive phase of sound-induced seizures: *A*—Rigid extension of tonic spasm; *B*—Spasmodic twitching at the clonic stage; *C*—Head lifting at the beginning of recovery.

SOUND-INDUCED SEIZURES IN RABBITS

JOSEPH J. ANTONITIS, DORCAS D. CRARY, PAUL B. SAWIN AND CARL COHEN*

IN a number of publications dealing with epileptic seizures in rabbits of the Vienna White race, Nachtsheim[5,6,7,8] noted that observed seizures were correlated with events such as the feeding of rabbits in their cages, cleaning and inspecting cages, wheeling a barrow before the cages, whistling shrilly in the vicinity, etc. Although Nachtsheim concluded that visual or auditory stimuli were, as a rule, the factors responsible for precipitating the epileptic attacks in the rabbits, he did not deliberately attempt to induce such attacks by exposing the animals to visual or auditory stimuli under controlled conditions. The present article describes the results obtained when two sublines of a race of white spotted rabbits, which also produced some "Vienna White-like" offspring, were tested to determine the nature of their reactions to a complex sound of relatively high intensity under controlled conditions.

Method and Subjects

Since Nachtsheim's observations and those of the authors indicated that practically any intense auditory stimulus sufficiently prolonged would precipitate epileptic-like attacks in genetically predisposed rabbits, it was felt that the bell-tub situation devised by Hall[4] for studying audiogenic seizures in mice could, with a few modifications, be adapted for the purpose of inducing seizures in rabbits. The test apparatus devised for the rabbits consisted of a wood box, 30 inches square on the inside, and 24 inches high. A clear 18 inch square plate glass pane in the front wall of the cage permitted observation of the behavior of the subject within. The interior of the cage, with the exception of the glass window and the floor, was lined with one-inch thick cotton quilting to minimize the possibility of self-injury by the subject in the event of seizure induction. An ordinary six-volt electric doorbell was affixed to the center of the hinged padded lid of the cage. During testing, the bell was activated by current from four one and one-half volt dry cells. Measurements of sound intensity at the floor of the test cage, made with an H. H. Scott Sound Level Meter, Type 410A, indicated a fairly uniform distribution of sound over the 30 inch square area. The mean of eight distributed peripheral measures and one central measure was 94.1 db R.M.S. sound pressure above 0.0002 dynes/cm.^{2} The range of intensity levels was 92 to 96.5 db.

The rabbits used in this study were from two sublines of the Ac race. The members of both sublines were all descended from three animals of an achondroplasia transmitter stock originally obtained in 1949 from Dr. Louise Pearce of the Rockefeller Institute. Later it appeared that certain members of the population descended from the three original rabbits suffered epileptic-like seizures under disturbing environmental circumstances. Some of these animals were bred selectively in such a way as to perpetuate this characteristic, and have become the AcEp subline. Others in which this character was not observed were bred without regard to this characteristic to perpetuate the original line desig-

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nated as Ac. Actually, certain individuals in the Ac line also transmit the seizure characteristic, but the incidence is less. In addition, both sublines have perpetuated characteristics resembling the "Vienna White" either in the heterozygous or homozygous state.[2] In this stock the homozygous individuals are white with blue eyes as described by Castle. The heterozygotes are marked with white over a range from three or four to 17 on Castle's scale.[2] Their eyes are blue, brown or heterochromic, with blue eyes ordinarily manifested only with the larger amounts of white spotting (range 9-17). This last characteristic is more suggestive of the white Dutch. Since Castle speaks of Vienna White and Dutch as being "cooperative," and since personal correspondence with Dr. Pearce indicates that both types were in the stocks at the Rockefeller Institute at the time the original animals were obtained, it is impossible at this time, without further breeding tests, to be certain we are dealing with the Vienna White gene alone, with white Dutch alone, or, what seems more probable, with both. The selection procedure which has resulted in the development of the Ac and AcEp sublines has been carried out without regard to the presence or absence of characteristics of pigmentation.

The available animals at the time the test was made were 36 of the AcEp line, including 18 males and 18 females 40 to 129 days of age, and 37 from the Ac line, including 20 males and 17 females 37 to 103 days of age. The environmental conditions under which the subjects were reared, i.e., housing, diet, handling, etc., were highly uniform for all.

Preliminary work indicated that the procedure generally used for inducing seizures in susceptible mice with the bell-tub[9] was also adequate for inducing seizures in susceptible rabbits in the test cage described above. The animal to be tested was transported in a carrying box from its home cage to the room containing the test cage. Ten seconds after the subject was placed inside the test cage, the bell was activated by closure of a knife-switch. Simultaneously, stop watches were started by two observers. Sound stimulation was continued for a period of 90 seconds except in instances of seizures. In the latter instances, stimulation was discontinued when the rabbit fell over on its side, signaling onset of the convulsive stage of the seizure. It should be noted here that preliminary work with several susceptible rabbits of the AcEp line definitely established that introduction of the rabbits to the test situation was not in itself the factor which provoked epileptic-like attacks. Some susceptible subjects were allowed to remain in the test situation for several minutes before onset of sound stimulation. In none of these instances did seizures occur prior to sound stimulation.

For the purposes of this initial exploratory experiment, it was decided to test each of the subjects once in the manner described above. Testing of the subjects occupied two successive days during the third week of June. This fact is mentioned, since Nachtsheim[8] reported a definite seasonal trend in the frequency of occurrence of spontaneous epileptic seizures in Vienna White rabbits—June being the month of highest incidence.

Observations

Table I shows frequencies of occurrence of epileptic-like seizures induced in the single test of reaction to sound in males, females and in both sexes of the two sublines. Although the number of subjects tested is not large and the range of ages is restricted, the animals have been further divided in Table I into two age groups on the basis of the range of ages represented to obtain a preliminary determination of the possible importance of the age factor. Chi-square tests show that none of the differences between frequencies of males and females "seizing" is statistically reliable. Other tests of significance do not reveal any reliable differences between frequencies of seizures in the two age groups. For a satisfactory determination of the degree to which age may govern seizure susceptibility in rabbits of these sublines, a more elaborate study in which a wider range of ages is represented is apparently necessary.

The difference between the frequencies of AcEp and Ac rabbits seizing in the total groups is not statistically significant ($\chi^2 = 2.88$, $P = .10\text{-}.05$). The fact that seizures occurred in both Ac and AcEp groups indicates that the selection procedure has not yet elim-

inated the seizure characteristic from the Ac subline but has reduced the frequency of its appearance to an almost significant extent.

The Sound-Induced Seizure Pattern

Table II, prepared from records taken by the observers during experimentation, provides a picture of the similarities and differences in the pattern of reaction among the subjects that suffered seizures.* This table presents individual and group mean times of occurrence and durations of successive distinguishable stages of the complete sound-induced seizure pattern. Since the number of Ac subjects that reacted with complete seizures was so small, the means listed for this group cannot be regarded as very reliable. Additional cases are needed to determine whether the two sublines differ reliably with respect to patterns of convulsive reactions as suggested by the data in Table II. Two subjects indicated in Table I as having suffered incomplete seizures are not represented in Table II. In these two instances the subjects reacted with wild running for a few seconds at the onset of sound and then did not seem further affected even though stimulation was continued for the full 90 seconds.

The seizure induced by sound in the rabbits bears a remarkably close resemblance to the spontaneous epileptic attack in the Vienna White rabbit as described by Nachtsheim[8] and also to the audiogenic seizures in the DBA mouse as described most fully by Vicari.[9] Three major stages were distinguished in the seizure pattern of the rabbit:

1) *Preconvulsive stage.* With the onset of sound, startle reactions were observed both in rabbits that did and did not convulse. After the initial startle reaction, susceptible rabbits either remained motionless for a few seconds or immediately began to move about the cage in a restless manner. A wild leap either from a motionless position or in the course of restless movement signalled the onset of the first or wild running phase of the seizure. The data in Table II suggest that the threshold of reactivity to sound may be lower in AcEp than in Ac subjects. The mean latency of wild running behavior, latency being measured from the time of onset of the sound stimulus to the instant of the first wild leap, was 6.8 seconds for the AcEp group and 17.0 seconds for the Ac group. The maximum latency of the wild running reaction was 28 seconds in the present group of seizure susceptible rabbits; the minimum latency about three seconds.

During the wild running phase which ranged in duration from about one second to about 16 seconds in the total groups of 16 reacting rabbits, the rabbits dashed around the cage frantically, striking the padded walls, squealing, and leaping high from time to time. At what appeared to be the peak of such activity, the subject suddenly fell over on its side and entered the clonic-tonic stage of the seizure.

2) *Convulsive stage.* Immediately upon falling, the subject generally exhibited a few kicking movements of the legs, then underwent a tonic spasm. During this spasm the back was arched inward, head was thrown back, forefeet were drawn up, and the hind legs were extended. This rigid extension was held for only a few seconds. Accurate timing of the first phase of the convulsive stage was not possible because of its short duration. The muscles of the subject were then observed to lose their rigidity and the fore and hind legs began to twitch and move spasmodically in the second or clonic stage of the seizure. Gradually the muscle spasms became less frequent and the subject simply rested motionless.

The latency of this stage was measured from the instant of onset of sound to the instant the animal fell over on its side; the duration of this stage was measured from the instant of falling over to the first observable sign of recovery. This took the form of lifting of the head. In a few instances head lifting coincided with standing upright. In the total group

TABLE I. Frequencies of sound-induced seizures in Ac and AcEp groups

		Ac			AcEp		
Age in Days	Sex	Number Tested	Number Seizing	% Seizing	Number Tested	Number Seizing	% Seizing
37-82	Male	14	2*	14.3	10	6*	60.0
	Female	12	2	16.7	7	2	28.6
	Total	26	4	15.4	17	8	47.1
83-129	Male	6	1	16.7	8	2	25.0
	Female	5	1	20.0	11	2	18.2
	Total	11	2	18.2	19	4	21.1
37-129	Male	20	3	15.0	18	8	44.4
	Female	17	3	17.6	18	4	22.2
	Total	37	6	16.2	36	12	33.3

*Each of these numbers includes one rabbit with an incomplete seizure.

*A motion picture record of the pattern of tse sound-induced seizure in the rabbit has been included in a recent film by Antonitis and Scott.[1]

of 16 reacting rabbits, latencies of the convulsive stage ranged between four and 35 seconds. The individual data in Table II indicate a wide range of variation in the durations of this stage—six seconds to 235 seconds.

3) *Recovery stage.* Latency of recovery as shown in Table II was measured from the onset of sound to the time the subject was first observed to move its head. The time at which the animal stood upright was taken as the time of complete recovery. The duration of the recovery stage was obtained by taking the difference between these two recorded times. Table II shows that six rabbits have zero time listed for the duration of the recovery stage. In these instances, head lifting coincided approximately with standing upright. The other rabbits recovered more slowly, recovery following a cephalocaudal sequence. First the animal would lift its head, then move its forefeet. Spasmodic unsuccessful efforts to move the hind legs generally preceded standing upright. In subjects that endured seizures of short duration, some lack of control over the movements of the hind legs was observed for a few seconds after the animals stood up. Table II shows a high degree of individual variation in the duration of the recovery stage, the range being 0 to 625 seconds. The AcEp group appears to be more variable than the Ac group both in terms of latencies and durations of this stage.

The last column of Table II presents the computed individual and group mean durations of the sound induced seizures. These durations of complete seizures were measured from the onset of wild running behavior to the time of complete recovery, i.e., standing upright. The data in this column suggest that susceptible AcEp's may be more variable than Ac's in terms of duration of seizure and may also be expected to occupy more time in undergoing the seizure than Ac's.

Inheritance

Nachtsheim[8] has concluded that seizures are determined by a single recessive gene. The limited data of this population are for the most part in harmony with this interpretation. Because of the small number of animals tested, no attempt was made to study the two sublines separately. Hybrid parents produced six seizure animals out of 27 progeny. Of six progeny obtained from parents both of which had spontaneous seizures, all had seizures. Eight such individuals in 32 progeny were from parents, one of which had previously seized, whereas its mate, to our knowledge, had never seized but had produced affected young, and therefore presumably was heterozygous. This mating is irregular insofar as a single recessive gene hypothesis is concerned. The discrepancy is perhaps explained by the fact that the numbers are small and that, as shown below, animals susceptible to seizures do not always react under the conditions of our test. Since it has been shown[3, 4] that in mice there are distinct racial differences in seizure susceptibility, such may also prove to be the case in rabbits, when adequate numbers of animals are available for testing.

Discussion

The results of this study have very definitely established that a complex sound of relatively high intensity will induce epileptic-like seizures in genetically predisposed rabbits. While the sound stimulus used appears to be adequate, further experimentation is necessary before any statement can be made regarding how closely the stimulus used achieves an optimal level of efficiency in terms

TABLE II. Individual and group mean times of occurrence and durations of the stages of the sound-induced seizures in AcEp and Ac rabbits. All latencies and durations are in seconds

Animal Number	Sex	Age in Days	Running Stage Latency (A)	Running Stage Duration (B)	Convulsive Stage Latency (A+B)	Convulsive Stage Duration (C)	Recovery Stage Latency (A+B+C)	Recovery Stage Duration (D)	Duration of Seizure (B+C+D)
AcEp									
8X23	F	40	10	1	11	16	27	0	17
7X87	M	44	5	2	7	47	54	2	51
7X88	M	44	11	4	15	10	25	0	14
7X89	M	44	6	1	7	113	120	8	122
7X90	F	44	3	2	5	90	95	15	107
7X91	M	44	3	1	4	46	50	0	47
4X66*	M	65	5	2	7	58	65	625	685
1X02	M	92	3	16	19	8	27	0	24
9X7	M	92	15	5	20	85	105	385	475
7W66	F	114	4	1	5	235	240	120	356
4W18*	F	128	10	2	12	105	117	348	455
AcEp Means		67.4	6.8	3.4	10.2	73.9	84.1	136.6	213.9
Ac									
8X83*	F	37	13	7	20	25	45	17	49
8X88*	M	37	21	1	22	37	59	9	47
8X50*	F	39	13	8	21	6	27	0	14
3X9*	M	97	28	7	35	20	55	0	27
4X1*	F	97	10	15	25	25	50	20	60
Ac Means		63.4	17.0	7.6	24.6	22.6	47.2	9.2	39.4

*White spotted animals. All others are blue-eyed white.

of frequency characteristics and intensity for inducing seizures in rabbits.

Following completion of the present experiment, the question was raised whether the procedure of testing the rabbits just once was adequate for detecting those susceptible to seizures. To obtain a preliminary answer to this question, ten 40 to 44 day old AcEp rabbits involved in the present study were retested on the day following initial testing. On the retest, one of the animals that convulsed on the initial test failed to convulse again, and two of the animals which did not convulse on the initial test did when retested. These two animals have not been included in Table II.* These results indicate that seizure susceptibility varies in the same rabbits from day to day to some extent and that a single test cannot be counted on to reveal all subjects with convulsive predispositions on any day. Considering the results of this pilot study and Nachtsheim's previously noted observations that seizure susceptibility may vary with age and time of year, in order to obtain accurate measures of differences in frequencies of occurrence of the seizure characteristic in populations of rabbits, it is necessary that all subjects be of approximately the same age and be tested for several days in succession following a procedure similar to that used by Fuller, *et al*[3] in working with populations of mice.

Since Nachtsheim[8] reported that as a general rule so-called "spontaneous" epileptic attacks in Vienna White rabbits appeared to be precipitated by disturbing environmental conditions, it may very well be that the majority of such seizures observed by Nachtsheim were actually sound-induced. The remarkable similarity between the pattern of the sound-induced seizure in the subjects of this study and that of the spontaneous epileptic attack as observed by Nachtsheim in his subjects has already been noted. The possibility that the seizures observed by Nachtsheim were audiogenic rather than spontaneous in origin does not lessen the similarity of the pattern of the convulsive seizure in the rabbit to the pattern of the human epileptic, a point which has been stressed by Nachtsheim.[8] Actually, the finding that convulsive seizures resembling human epileptic seizures may be induced with ease in susceptible rabbits may have some practical value in the preliminary testing of pharmacological agents for protective properties. The genetically predisposed rabbit by virtue of its greater size and viability under seizure stimuli may be better adapted for such test purposes and for studies of physiological mechanisms underlying convulsive behavior than either the seizure susceptible mouse or the rat.

Nachtsheim's observations suggest that disturbing visual stimuli may also have served to precipitate the epileptic attacks in his subjects. Whether disturbing visual stimuli in and of themselves may provoke seizures in susceptible rabbits or whether unusual visual stimulation may simply function so as to lower the threshold of susceptibility to sound will have to be determined by further experimentation.

Summary

Seventy-three rabbits, 37 to 129 days old, in two sublines of a race of white spotted rabbits which produced some "Vienna White-like" offspring and in which spontaneous epileptic-like seizures had been observed, were exposed to relatively intense auditory stimulation under controlled conditions. Eighteen or 24.7 percent of the group suffered seizures, the seizures being comparable to spontaneous seizures observed by Nachtsheim in the rabbit and to audiogenic seizures in the mouse as described by Vicari. In the group tested the factors of age, sex and subline were not found to have any significant influence on the frequency of occurrence of seizures. Analysis of the pattern of the seizure in the two sublines led to the tentative conclusion that susceptible subjects of the AcEp subline have a lower threshold of reactivity to sound and are more variable than susceptible subjects of the Ac subline with respect to durations of stages of the seizure and of the complete seizure. Further observations indicate that a single test is inadequate for detecting all susceptible animals. Although numbers are small, with possibly one exception, the observations seem to support Nachtsheim's interpretation of inheritance by means of single gene substitution, seizure susceptibility being recessive.

The possibility that there may be distinct racial differences determined as in mice by other modifying factors, genetic or environmental, is being investigated further.

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*The two rabbits in question were males of the AcEp group. Latencies of the running stage, convulsive stage, and recovery stage for the two rabbits were 8 and 33 seconds, 10 and 35 seconds, and 85 and 62 seconds respectively. Durations of the three stages in order were 2 and 2 seconds, 75 and 27 seconds, and 9 and 123 seconds respectively. Durations of seizures were 86 and 152 seconds respectively for these two rabbits.

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(Received April 29, 1954)

CLINICAL GENETICS

THE materials and methods of human genetics have now reached the point where a considerable application to the medical fields is both possible and desirable. As one part of this synthesis, the volume edited by Sorsby was planned as "a contribution to clinical pathology."

The first one-fourth of the book discusses genetic theory, including such topics as penetrance and expression, the detection of carriers, twin studies, linkage, and biometric analysis. This section contains many valuable suggestions which should be considered in the planning or evaluation of studies in human genetics. The remainder of the volume presents clinical and genetical details for each of the organ systems, including many tables, photographs, and pedigrees (mostly from previously published work). Some parts of this latter section are less adequate from the genetic point of view.

One of the principal values of joint authorship is that details and points of view, which otherwise would be widely scattered, are collected in one volume. However, this potential advantage was not fully achieved because of the differences in adequacy of treatment.

For example, there appear to be differences of opinion as to what constitutes valid evidence of genetic influence. Some authors describe only those conditions for which the evidence is highly reliable, while others include conditions on the basis of such indirect evidence as multiple involvement, early onset, association with other known inherited (or congenital) dysplasias, presence in both members of one pair of identical twins, or a few cases of familial occurrence. Some of these may suggest a genetic relationship, and the inclusion of these conditions may stimulate further research. Nevertheless, it would seem essential at this stage in the synthesis of clinical and genetical data that the relative certainty of genetic influence should be clearly indicated for each type of pathology.

There are also variations in terminology. "Sporadic" is sometimes used in a way which appears to exclude heredity, and "familial" in a sense which is equivalent to "genetic." The phrase "hereditary disposition" is loosely used. The term "phenocopy" is used in two quite different senses on pages 15 and 361. The problem of terminology is particularly important in a book which probably will be widely quoted.

On the other hand, most of the chapters contain a concise and critical evaluation of a large amount of material, in a form probably not available from any other source. Any research worker in these fields must be fully aware of the qualifications and the limitations which are discussed. The suggestions for needed research will be valuable. In addition, the way in which the book is accepted by clinicians will provide a basis for planning revisions or other books in an attempt to develop the best presentation of genetics in the clinical fields.

Among the many features which the reviewer appreciated were the following: the tabular presentation of a large volume of material, and the estimate of the reliability of observation (as in chapter 3); the good adaptation to a clinical audience (as in chapter 7); and the sub-headings for genetic data, the relatively larger space given to those conditions better understood genetically, and the empiric risk figures (as in chapter 21).

Each chapter has a selected bibliography. In about half of the chapters, some of the papers which are cited in the text do not appear in the bibliography. Again, in about half of the lists, the titles of the papers are omitted. Some of the longer lists have the more important references marked by an asterisk.

This book will without doubt become a first point of reference for many workers. However, in view of the variability in treatment of the topics and the high price of the book, some potential purchasers may want to borrow a copy first to find out if their particular fields are adequately represented.

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**Arnold Sorsby*, editor. Clinical Genetics. Butterworth & Co. (Publishers), Ltd., London. (C. V. Mosby Company, St. Louis.) 580 pp. $17.50. 1953.

HAPLOIDY IN CASTORBEANS

D. Donald Poole and H. H. Hadley*

NORMAL AND HAPLOID CASTORBEAN PLANTS
Figure 12

A haploid plant of variety USWA 74 at the right is compared with a normal diploid plant at the left. The small leaves, and the absence of capsules are characteristic of haploid castorbeans.

DURING the past year several abnormal castorbean plants, *Ricinus communis* L., were observed in the breeding nursery and in commercial fields at Chillicothe, Texas. These plants were characterized by small leaves, numerous inflorescences and almost complete sterility. It was surmised that they might be haploids. One plant, R. A. 176-2-2, originating from selfed seed of P. I. 183468† was analyzed cytologically. Pollen mother cell prepara-

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†Plant Introduction number 183468.

COMPARISON OF HAPLOID AND DIPLOID CASTORBEAN RACEMES

Figure 13

The plant at the left is a normal diploid of R.A. 176-2-2. Note the open male flowers at the base of the raceme and the extended spines on the ovary. A good capsule set is seen at the bottom. In comparison, the plant on the right is a haploid. Note the absence of capsules and the failure of the opening of male flowers.

tions of this plant revealed 10 univalent chromosomes at metaphase verifying the haploid condition.

Description of the Haploid Plants

The haploid castorbeans are very similar to normal plants in height, stem size and growth habit, but they can be distinguished easily from normal plants by their small leaves, and highly sterile racemes (Figure 12). The male flowers seldom open (Figure 13). The few that do open usually do so in the cooler weather of early fall. There is a very hard fusion layer between the male floral bracts and only a few stamens succeed in elongating sufficiently to extend through the bracts. The anthers of the haploid do not dehisce and pollen formed in these anthers is empty and collapsed although an occasional filled grain is found. The pollen appears only slightly smaller in size than diploid pollen and does not stain with iodine. Female flow-

ers appear normal in most respects except that the ovary spines are greatly reduced. The female flowers for the most part are sterile, although an occasional seed is found on some racemes. Excessive, prolific raceme development of the haploid is characteristic and is probably caused by incomplete seed set similar to prolific raceme development seen on normal plants grown under drought conditions.

Cytological Observations

Chromosomes in both the diploid and the haploid castorbean plants, which were observed cytologically, were small and difficult to study. Metaphase I chromosomes, however, were sufficiently distinct to obtain accurate counts and evidence of the type of chromosome association.

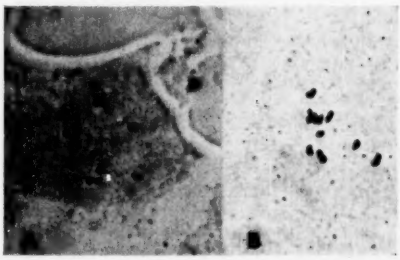
During prophase I, chromosomes were found to be synapsed in the diploid, but in the haploid no such pairing was observed. At this stage the material was too unfavorable for studies of chromosome morphology. At metaphase I, 10 bivalents were observed in the diploid. In some cells bivalents were very close together but no definite multivalents were observed. In the haploid at metaphase I 10 small, rounded univalents were observed. Although in a few cells two univalents were in close proximity (see Figure 14), they did not appear to be paired. Thus there was no good evidence for duplicate segments in this castorbean material.

During anaphase I the chromosomes of the haploid apparently moved at random giving irregular distributions such as 4-6 and 3-7. No division of univalents such as reported in wheat[3] was noted. No chromatin bridges were observed. The second meiotic divisions in the haploid appeared to be more regular than the first.

Discussion

Cytological behavior of abnormal castorbeans was investigated to verify the supposition that haploidy occurs in castorbeans much as in other plants.

Blakeslee[1] has reported finding haploids in *Datura*. Other haploids have also been found in several dicotyledonous genera and in a number of grasses. Haploids in grasses have been found following treatments with high and low temperature and after X-ray treatment.[5, 7, 9] A number of haploids have been found in twin-stalked grass seedlings.[8] Christensen and Bamford[2] suggested a practical utilization of pepper haploids in the development of homozygous diploid lines for breeding material. Toole and Bamford[10] later reported a method by which fertile diploids were produced successfully from these haploid peppers. Morgan and Rappleye[6] suggested the utilization of the colchicine method in the isolation of new homozygous diploid varieties.



MEIOSIS IN HAPLOID AND DIPLOID PLANTS

Figure 14

A—Metaphase I or early anaphase of haploid castorbeans showing 10 univalents. *B*—Metaphase I in a comparable diploid showing 10 bivalents. (Approximately 1000×).

Hagerup[4] first reported the diploid chromosome number of *R. communis* to be 20. Haploidy in *Ricinus* apparently has not been previously reported. Haploids have been found at Chillicothe, Texas in the USDA 74 variety and several other lines in the breeding material in addition to the one reported above. However the frequency appeared to be very low. In all cases these haploids were single plants rather than twin-stalked seedlings. Possible utilization of Toole and Bamford's[10] method with castorbean haploids might well be of value in developing inbred lines for use in commercial hybrid production.

Summary

The observation of haploids in castorbeans, (*Ricinus communis* L.) is reported. Chromosome behavior in castorbean haploids is similar to that found in other genera. Cytological analysis of meiosis revealed 10 univalent chromosomes at first metaphase.

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(Received February 19, 1954)

◆

A METHOD OF KEEPING A FLEXIBLE PEDIGREE CHART

NORIO MITSUOKA*

IN the course of maintaining a breeding program of a Japanese strain of laboratory rats in connection with a tumor-host research project, it became desirable to have available a method for quickly tracing the lineage of individual animals. The usual records kept of our animals supplied the necessary information but a great deal of time was consumed in going back into the files to work out relationships. Pedigree charts, after several generations, became much too involved and cumbersome. Therefore, the method described herein was devised in order to present at a glance and in a conveniently handled manner, the family history of any given individual.

The method consists of employing separate strips of cardboard to represent individual animals and fixing these to each other with paper fasteners in order to make a flexible form of the pedigree charts. Only the females of each line have been represented in our charts. The males to which they have been mated are identified on each individual strip. However, the method may be adapted to include males and females. As inbreeding progresses, certain sublines are lost or discarded. Strips representing these individuals may be readily removed from the pedigree tree leaving only those currently in existence. The tree takes the form of a straight line of descent when the strip of an individual in question is held in one hand, while tension is applied, as the strip representing the original breeder of the subline is held in the other hand.

Gray colored pressboard cut into strips ⅞ by 2½ inches and punched with an office two-hole punch was used in our charts. A simple code was devised giving certain desired information concerning each individual. The type of information and code would, of course, depend upon the interests of the laboratory.

FLEXIBLE PEDIGREE CHART

Figure 15

See text for explanation.

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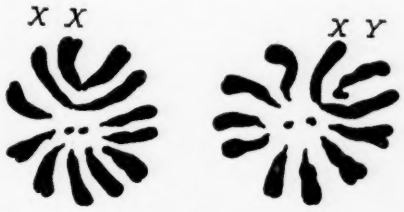
LETHAL-POLYPLOID—A POLYPLOID GENE IN DROSOPHILA HYDEI

HANS GLOOR AND HANSRUDOLF STAIGER*

FOLLOWING cold treatment a small percentage of *Drosophila hydei* larvae were found to contain in the central nervous system numerous mitotic cells exhibiting various degrees of polyploidy.[1] It was first believed that the treatment had caused this abnormality, but since the larvae were from a wild type strain from Rabat, Morocco, and since a similar effect could not be reproduced in larvae of another wild type strain from a different region (Zurich, Switzerland), it was suspected that some genetical mechanism might be responsible for polyploidy in the larvae. Among larvae of *D. hydei, melanogaster* and *simulans* kept at low temperatures (5 to 10° C.) only a general contraction of chromosomes in metaphase could be obtained, and only occasional individual polyploid mitoses were found. However, Mickey and Blount[2] found cold shock treatment (—3.3 to —6.1° C.) effective in producing polyploid cells in *Drosophila* larvae as well as in embryos.

It was then found that the abnormality in *D. hydei* is caused by a single Mendelian recessive, which had been present at a low frequency in the original stock. As an introduction to the present report on the genetical analysis of this trait, its phenotypic effects are briefly described.[3]

The first indications of abnormality are found during the second day (at 23° C.) of larval development. Some of the neuroblast mitoses in affected larvae are arrested in metaphase with the chromosomes greatly shortened. The effect seems to be caused by a disturbance in the spindle mechanism and is similar to that induced by specific inhibitors such as colchicine. In older larvae a striking accumulation of metaphases is found



NORMAL METAPHASE

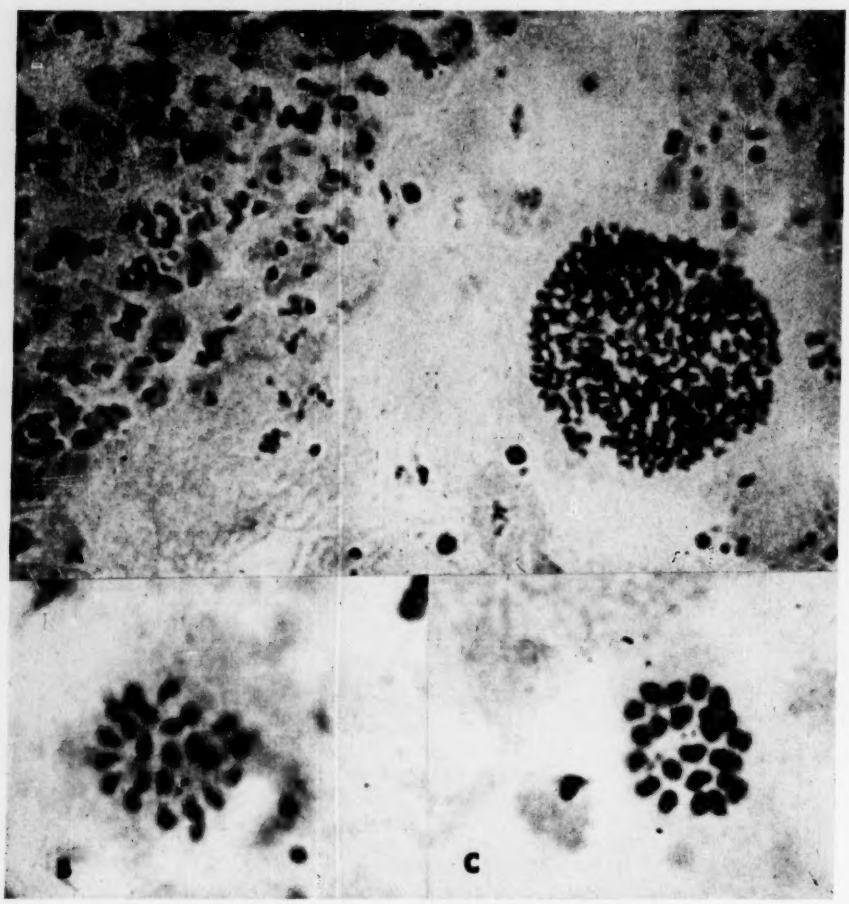
Figure 16

Normal metaphases in *Drosophila hydei*, female left and male right, from aceto-orcein squash preparations of larval brains. (Approximately 3800×).

(Figure 17*A*), mostly of a diploid and tetraploid nature and invariably with the chromosomes shortened. In Figure 16 the normal chromosome complement in male and female metaphases can be seen. Figure 17*B* and *C* shows tetraploid metaphases. Higher degrees of ploidy, mostly 8- and 16-ploids, are less frequent (Figure 18). Some of the large ganglion cells reach a degree of polyploidy which is too high even to estimate, containing thousands of chromosomes (Figure 19). An accurate count of chromosomes is sometimes possible in polyploid cells up to 16 *n*, and it is found that aneuploids and triploids also occur.

The metaphase chromosomes in polyploid cells are often arranged in a roughly spherical pattern (Figure 17*A*) although regular arrangement and anaphase movement can sometimes be seen. With increasing numbers of chromosomes the metaphase arrangements tend to be completely disrupted (Figure 18*C* and 19). At later larval stages many nuclei, regardless of their degree of polyploidy, undergo pyknotic degeneration.

*Institute of Zoology and Comparative Anatomy, University of Zurich. The work has been supported by a grant from the Georges und Antoine Claraz-Schenkung. The junior author is holding a fellowship of the Janggen-Pöhn Stiftung. The authors wish to dedicate this paper to Professor Fritz Baltzer, University of Berne on the occasion of his 70th birthday.



DIPLOID, POLYPLOID AND TETRAPLOID METAPHASES

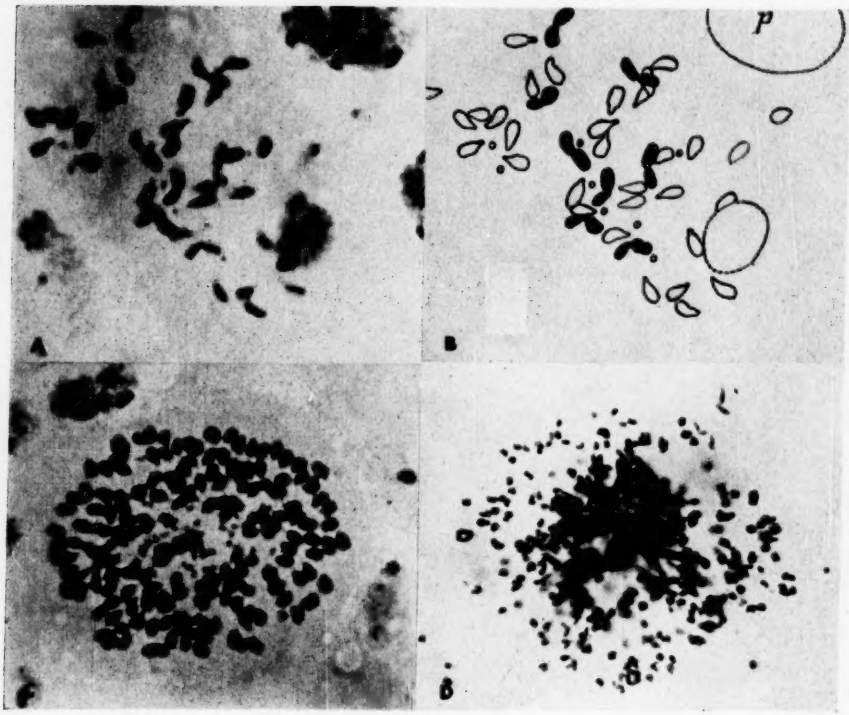
Figure 17

Some aspects of mitosis in larval brains of the *lpl*-mutant of *Drosophila hydei*. *A*—Arrested (diploid) metaphases and one highly polyploid metaphase. 850×. *B*—Tetraploid metaphase in the female. *C*—Tetraploid metaphase in the male. The dot chromosomes have been retouched. Aceto-orcein squash.

Whereas polyploid larvae as a whole grow normally—their larval tissues exhibit normal nuclei with polytenic chromosomes—growth in the rudiments of imaginal organs including the brain is retarded. In these imaginal organs polyploidy as described above develops, and in addition their structure is in varying degrees abnormal, probably due to the large numbers of degenerating cells. Metamorphosis is prevented and the polyploid individuals die either in the late larval stage or shortly after pupation.

Genetical Analysis

Of 89 individual pair matings (IP) the F_1 generations were tested cytologically. Polyploid larvae occurred among the offspring of



POLYPLOID MITOSES

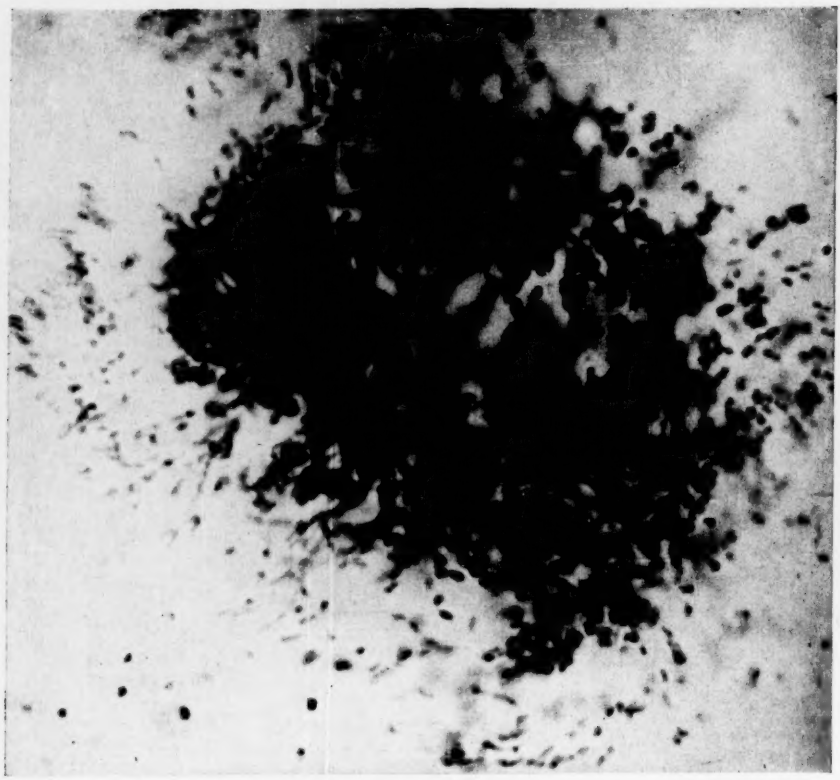
Figure 18

Polyploid mitoses in *lpl*-larval brains. Aceto-orcein squash preparations. *A* and *B*—Octoploid early metaphase in the female. X-chromosomes are shown in black, p = polyploid interphase nucleus with several chromocenters. *C*—Highly polyploid metaphase plate, probably *32 n*. Dot chromosomes have been lightly retouched. *D*—Highly polyploid metaphase with chromosomes arranged irregularly. All figures approximately 2500×.

five matings, the proportion of polyploids ranging from 10 to 26 percent. On the assumption that the polyploid character might be due to a recessive lethal, *lpl*, IP matings were made from one culture in which 27 polyploids were found from a total of 106 larvae examined. If our assumption should be correct, we would expect both parents to be heterozygous, +/*lpl*. The genotypes +/+, +/*lpl*, *lpl*/*lpl* would then be expected to occur in a 1:2:1 ratio in the F_2. Selected at random from the viable types +/+ (1/3) and +/*lpl* (2/3), individual pair matings would be expected to yield polyploid larvae in four-ninths of the cultures. Experiments of this kind were repeated over a number of generations using only those cultures for further breeding which had produced *lpl* larvae among their offspring. The individual results (Table I), except for

TABLE I. Results from 13 generations of pair matings. The parents in each generation were selected from those individual pair matings which had yielded polyploids (*lpl*/*lpl*) among their offspring.

Generation	Cultures with *lpl*	Cultures without *lpl*	Sterile cultures
1	24	24	?
2	33	62	10
3	17	24	4
4	20	21	9
5	10	17	5
6	10	13	2
7	23	24	8
8	15	20	2
9	31	39	11
10	7	7	1
11	13	13	3
12	8	12	9
13	88	106	31
Total	299	382	



GIANT GANGLION CELL

Figure 19

Giant ganglion metaphase cell of *lpl*-larvae, with an extremely high degree of polyploidy. Aceto-orcein squash, 1900×.

the second generation are in fairly good agreement with an expected 4:5 ratio. For the total result, the chi-square test gives a probability of $P > 0.70$.

In a second experiment, the offspring of IP cultures, which had produced only normal larvae, were tested. Among 24 mass cultures, 15 produced polyploids and nine did not. Of the parental pairs four-fifths are expected to contain the *lpl* gene in one parent while in the remaining one-fifth both parents would be homozygous for the normal allele. Mass cultures of their offspring are expected to yield no *lpl* larvae in one-fifth of the cases, whereas four-fifths should produce homozygous *lpl* larvae. Among 24 mass cultures tested, polyploidy was found in only 15. However, if Yates' correction for continuity of the chi-square test is used, the observed ratio of 15:9 does not significantly differ from the expected proportion of 4:1.

Provided that viability of polyploids up to late larval stages is normal, the proportion of polyploid larvae is expected to be 25 percent if both parents are heterozygous, *lpl*/+. In 23 IP cultures producing polyploids, varying numbers of larvae were examined cytologically (Table II). In no case was there a significant deviation from the expected 3:1 ratio.

All the data clearly indicate that the type of polyploidy described is produced by a single recessive Mendelian factor. Since larvae homozygous for this gene are unable to undergo metamorphosis and die at the end of the larval period, the symbol *lpl* (lethal polyploid larvae) is proposed.

In an attempt to determine the location of the gene for the *lpl* mutation, it was first ascertained that there is no sex linkage. With the autosomal recessive mutants *e* and *p** crosses were then made as follows: *e/e* × *lpl/+* and *p/p* × *lpl/+*. From the first generation offspring IP matings were made among those which yielded *lpl/lpl* larvae and *e/e* or *p/p* flies, both parents being heterozygous for *lpl* and the marker gene. The following generation was bred in IP matings using only flies which were phenotypically wild type. Among these cultures a proportion of four-ninths yielding polyploid larvae would indicate independent segregation whereas a proportion significantly exceeding the usual ratio would indicate linkage between *lpl* and the marker gene. The results were such that independent segregation must be assumed in both cases. Unfortunately it has not been possible to obtain any other mutant stocks of *D. hydei*. As a result, only the X chromosome has so far been excluded and chromosome 2 (ebony and peach) made unlikely as the carrier of the *lpl* gene.

TABLE II. Proportion of normal and polyploid larvae among the offspring of individual pair matings between heterozygous parents. Probabilities as indicated by the chi-square test

Number of larval brains examined	Normal	Polyploid	P > than:
108	82	26	0.8
128	95	33	0.8
78	55	23	0.8
93	72	21	0.5
61	49	12	0.3
71	52	19	0.7
52	37	15	0.5
109	83	26	0.8
68	55	13	0.2
106	72	34	0.05
73	57	16	0.5
100	75	25	1.0
60	40	20	0.1
47	37	10	0.5
69	45	24	0.05
134	96	38	0.3
80	62	18	0.5
52	36	16	0.3
89	63	26	0.3
44	29	15	0.1
88	63	25	0.3
98	74	24	0.9
102	78	24	0.7
Total	1407	503	0.15

Summary

"Lethal-polyploid" (*lpl*) is an autosomal recessive lethal in *Drosophila hydei*, not linked with chromosome 2 genes *e and p* (the only mutants available). In homozygous condition *lpl* affects mitosis in postembryonic stages mainly by blocking the spindle mechanism, thereby producing polyploid cells in the central nervous system and imaginal rudiments.

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*Ebony and peach kindly furnished by Dr. A. H. Sturtevant.

(*Received March 5, 1954*)

◆

ON THE REDISCOVERY OF MENDEL'S WORK BY HUGO DE VRIES

Th. J. Stomps*

DURING the last Genetics Congress at Bellagio I got the impression, that outside Holland the true and exact story of the rediscovery of Mendel's work by Hugo de Vries is not accurately known. I was even shocked by the utterance of one of the members that it appeared that in the beginning de Vries had been dishonest and had tried to hush up the name of Mendel. Several members asked me to publish what I knew of the true situation through my personal acquaintanceship with de Vries. For that reason I wish to say a few words here about this matter.

In 1889 de Vries discontinued his studies on osmosis and plasmolysis and published his "Intrazellulare Pangenesis"—the real starting

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point of modern genetics, in which the term "pangene" was coined for the bearers of the separate hereditary characters. (This word was not created by Darwin, as Johannsen erroneously wrote in the first impression of his book and is still sometimes believed.)* Thereupon de Vries undertook his experimental work in the garden, with the result that a long series of genetical papers already appeared before 1900. He made numerous crosses between species and varieties and, being unaware of the existence of Mendel's paper, "Versuche über Pflanzenhybriden," quite independently discovered the formula, which we now know as Mendel's law. In 1900, at just the time he was about to publish the results of his experiments he received a letter from his friend Professor Beyerinck at Delft, reading thus: "I know that you are studying hybrids, so perhaps the enclosed reprint of the year 1865 by a certain Mendel which I happen to possess, is still of some interest to you." De Vries read the paper and found that the results of his experiments, which he had believed to be quite new, had already been reported 35 years before. And it goes without saying that in his first article referring to the subject under discussion, "Das Spaltungsgesetz der Bastarde," received by the editorial staff of the *Deutsche Botanische Gesellschaft* on the 14th of March and published on the 25th of April 1900, the work of Gregor Mendel was accurately mentioned. This then is the true story of the rediscovery of Mendel. I once asked De Vries whether he could remember the precise moment at which he discovered Mendel's now famous paper, and he personally related the story to me. After the death of Beyerinck, I received remarkable proof of the exactness of his words: his family sent the reprint in question again to our institute, this time to me as its director, with the words that the right place would be the library of the Botanical Institute at Amsterdam, where indeed one can see it today in a special showcase.

The belief that deVries could have been dishonest in the beginning, is due to a rather unkind article by Correns, which appeared one month later in the next number of the *Berichte der Deutschen Botanischen Gesellschaft*. The unfortunate incident happened in this way: A few days after dispatching his first article, de Vries decided to send a short notice about his work to the *Comptes rendus de l'Academie des Sciences* at Paris. This paper, "Sur la loi de disjonction des hybrides," (presented to the Academy on the 26th of March) is merely a translation of the summary of the results of deVries' first article, in which the name Mendel was not repeated. According to Correns, he received a reprint of de Vries' summary on the 21st of April, which was unfortunately a few days before de Vries' original article appeared in the *Berichte*. Immediately Correns wrote his own article (mentioned above) at the end of which, however, he could have mentioned de Vries' German article, as in the meantime he had also received this article. In no instance should it be thought that de Vries discovered Mendel's work as early as 1892, simply because his (Mendel's) article was mentioned in Professor Bailey's book on Plant Hybridization. De Vries undoubtedly saw it listed in that volume and also in Focke's "Pflanzenmischlinge," but who would ever think of attempting to locate a popular magazine published by an obscure natural history society? It was without a doubt Beyerinck's reprint that made it possible for de Vries to take cognizance of Mendel's work.

Perhaps I may add a few words about the above-cited article by Dawson and Whitehouse. A very interesting point is that from the beginning de Vries defended the idea that the genes, as we now use the term, may occur in different conditions. He speaks of an active state and an inactive or latent one, also of semiactive, semilatent and labile pangenes. We now call such differences alleles (from the Gr. allos-different) and speak of a multiple allelomorphism. Therefore it is clear that from the beginning the term "gene" has been a collective term and I do not see how Dawson and Whitehouse could state that the collective usage of the term "gene" first appeared in 1939. Of course, when a gene has mutated, e.g. from the active to the latent state, it has become another gene, and it is therefore quite correct to say: "The genes B and B^+ are spoken of as alleles" or "Data on the segregation of the genes P and p are summarized." However, I do not see any confusion here and would reject the necessity of a new term "panallele." Of course, it is incorrect to speak of a gene as being heterozygous or homozygous: a plant or an animal may be heterozygous or homozygous for a certain character but certainly a gene cannot!

*G. W. P. Dawson and H. L. K. Whitehouse. The use of the term "gene." *Jour. Genet.* 50:396. 1952.

FRUIT AND LEAF CHARACTERS IN SUMMER SQUASH

The Interrelationship of Striped-fruit and Mottled-leaf

JOHN SCARCHUK*

THE literature on the striped-fruit character in summer squash, *Cucurbita pepo* L., is meager and inconclusive. Sinnott and Durham[4] have noted a striped character in fruit and reported on its inheritance. Their findings have led them to state: "Striped plants have always bred true to striping after it appeared, thus indicating that it behaves as a recessive character." They went on to say: "The stripe seems merely to be a region in the fruit where the dominant body color is inhibited in its expression and where the recessive color is thus able to manifest itself." Shifriss[3] found: "The inheritance of the striped-color types of group VI is not known but the heterozygotes which the writer produced by crossing striped and non-striped strains were always striped."

The literature on the mottled-leaf character in *Cucurbita pepo* L. is lacking but Scott and Riner[2] have reported on this character in *Cucurbita maxima*, Duch. They found that the mottled-leaf character is inherited as a dominant Mendelian character giving a 3:1 segregation in the F_2 progenies.

The breeding work carried out at the University of Connecticut Vegetable Research Farm at North Coventry included squash varieties of striped and uniform colored fruit, and mottled and uniform green leaf. Mottled-leaf may prove to be of value as a marker in the study of possible linkage relations, because it is one of the few vegetative characters that can be easily recognized. No linkage studies have been attempted, so this report deals with the inheritance of striped fruit and mottled leaf.

Materials and Methods

The parent lines Caserta, a new University of Connecticut introduction, and Early Prolific Straightneck were inbred at least five generations, sufficient enough to give very uniform progenies. Early Prolific Straightneck is a squash of the summer crookneck and straightneck group with uniform yellow fruit and uniform green leaves. Caserta is a Cocozelle type of the Italian vegetable marrow group with light green fruit striped with darker green, and having mottled leaves.

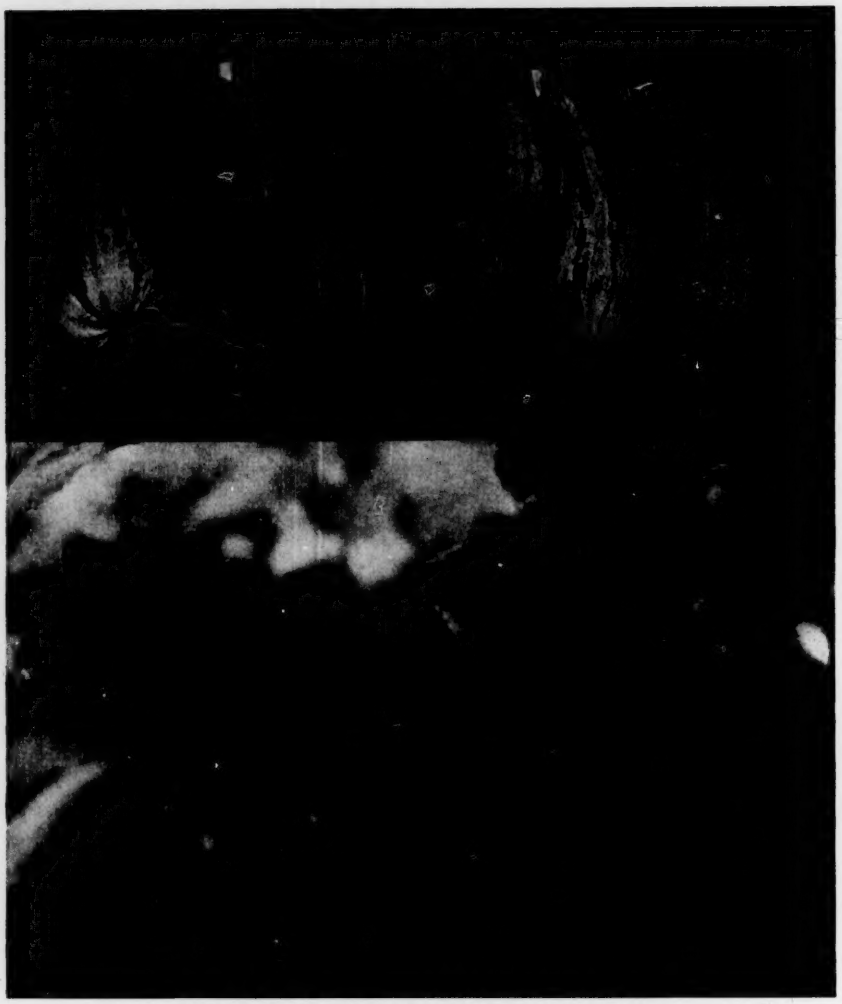
The striped-fruit character (Figure 20) in Caserta appears as longitudinal dark green stripes on an overall pattern of lace work of lighter green background. The pattern of the dark green stripe may be more or less continuous longitudinally or broken in longitudinal patches.

The mottled-leaf character (Figure 20) in Caserta is a scattering of light-colored silvery green patches located characteristically in the axils of the veins of the darker green leaf. They are visible only

TABLE I. Segregations in the F_2 progenies for leaf color, fruit color, and fruit pattern and their interrelationships

Phenotypes	No.	Probable Segregation	X^2	Probability (P)
M–	82	3		
mm	29	1	.075	.70–.80
Y–	76	3		
yy	34	1	2.048	.10–.20
St–	79	3		
stst	31	1	.593	.30–.50
M–Y–	56	9		
M–yy	25	3		
mmY–	20	3		
mmyy	9	1	2.162	.50–.70
M–St–	57	9		
M–stst	24	3		
mmSt–	22	3		
mmstst	7	1	1.030	.70–.80
St–Y–	50	9		
St–yy	29	3		
ststY–	26	3		
ststyy	5	1	7.592	.05–.10
M–St–Y–	37	27		
M–St–yy	20	9		
M–ststY–	19	9		
M–ststyy	5	3		
mmSt–Y–	13	9		
mmSt–yy	9	3		
mmststY–	7	3		
mmststyy	0	1	9.683	.20–.30

*College of Agriculture, University of Connecticut, Storrs, Conn.



STRIPED-FRUIT AND MOTTLED-LEAF SQUASH

Figure 20

At the top is shown the striped-fruit character in the Caserta variety, which appears as longitudinal dark green stripes on an overall pattern of lighter green. Below is shown the mottled leaf character, which consists of a scattering of silvery green patches located in the axils of the veins of the darker green leaf.

on the upper surface of the leaf. The mottling effect was found to be due to the cell structure of the palisade layer.[1]

The genetic study was started in the field with the crossing of the two parents. The F_1 progenies were grown in the greenhouse where they were selfed to give F_2 seed. The F_2 progenies were grown in the field in 1951 where counts were made.

Names and Symbols

Striped fruit instead of mottled fruit as used

synonomously with striped fruit by Shifriss[3] is suggested as the name for this character, and *St* and *st* as the dominant and recessive alleles respectively. The mottled-leaf character and symbols *M* and *m* as used for *Cucurbita maxima* Duch. by Scott and Riner[2] should appropriately be used for the same character in *Cucurbita pepo* L. *Y* and *y* are the dominant and recessive alleles for yellow and green fruit color respectively as used by Sinnott and Durham.[4]

Results and Discussion

In addition to the striped and uniform fruit color characters and mottled-leaf and uniform-green leaf characters, yellow and green fruit color characters are included in this study to give validity to the study of their inheritance. The segregations of the F_2 populations are shown in Table I.

The study of the segregations presumably controlled by a single pair of allelic genes showed a close 3:1 fit of mottled vs. uniform leaf, yellow vs. green fruit, and striped vs. uniform fruit. A study of the segregations controlled by two pairs of allelic genes showed a close 9:3:3:1 fit of mottled-leaf and green fruit vs. uniform green leaf and yellow fruit, mottled-leaf and striped fruit vs. uniform green leaf and uniform fruit color, and striped and green fruit vs. uniform and yellow fruit. The study of the segregations involving the three pairs of allelic genes showed a close 27:9:9:9:3:3:3:1 fit.

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(Received January 25, 1954)

◆

Extrinsic Influences on Leukemia

FACTORS present before birth may cause leukemia, a fatal cancerous condition of the blood to which both man and animals are subject, according to a three-year study recently completed by Dr. Elizabeth Fekete and Miss Hope Otis of the Roscoe B. Jackson Memorial Laboratory, Bar Harbor, Maine. The research, supported by a grant-in-aid from the American Cancer Society, dealt with the effects of extrinsic influences on leukemia. A report on the findings appears in the July issue of *Cancer Research*, and states that genetic tendencies to the disease were not modified by altering environmental conditions.

Two new lines of inbred mice were developed for the experiments. One line was derived from high-leukemic animals which were nursed by low-leukemic foster mothers; the other line was derived from mice born from fertilized ova of high leukemic females which were transferred into the uteri (wombs) of low-leukemic mothers and were subsequently born and nursed by them. Eighty-three percent of the foster-nursed mice developed leukemia, and 80 percent of the mice born from transferred ova developed leukemia. In both cases, the rate of leukemia was just as high as it is in animals of the same genetic background which are not separated from their natural mothers.

There are scientists who theorize that leukemia is caused by some filterable agent which is passed on from parent to offspring. This is true in the case of breast cancer in mice which has been found to be transmitted by some agent in the mother's milk.

The Jackson Laboratory investigators cannot say from the present study, that there is no filterable agent in the case of lymphatic leukemia. They do, however, state that if leukemia is caused by such an agent, that agent must be present in the germ cells. Neither nursing by low-leukemic foster mothers nor the combined influence of nursing and uterine environment of low-leukemic mothers, altered the incidence of leukemia.

FASCIATED PLANTS OF TWO VARIETIES

Figure 21

A—Fasciated plant of the Fairfax variety of the strawberry showing a fruit stem nearly two inches wide. All berries borne by the plant were worthless. *B*—Partly fasciated plant of the Eleanor Roosevelt variety of the strawberry showing small leaves on fasciated part (background) and large leaves on normal crown (foreground).

FASCIATION IN THE STRAWBERRY

Inheritance and the Relationship of Photoperiodism

GEORGE M. DARROW AND H. A. BORTHWICK*

AMONG the undesirable characteristics affecting the strawberry, particularly in the Middle and South Atlantic States, is fasciation, an enlargement and flattening of the fruit stem and fruit, giving a witches'-broom-like appearance to the plants. Because the principal varieties grown in the South are immune from, or highly resistant to this defect, it is not generally considered important. However, when new varieties are tested in that region, it may limit their culture there. The Fairfax, Heflin, Howard 17 (*Premier*), Dorsett, Sparkle, Catskill, Fairmore, Redstar, and other varieties are susceptible to fasciation, and losses to growers of these varieties have sometimes been serious. Affected plants produce little marketable fruit. Fasciation is a basic characteristic to be considered in breeding work because affected seedlings do not produce runners and therefore a large number of plants of susceptible selections may be affected and must be discarded. This paper summarizes the available information on fasciation. Most of the records and observations hold true for conditions found in North Carolina and Maryland. The experimental work which indicates photoperiodism as a controlling condition was done at Beltsville, Maryland.

Description of Symptoms

Fasciation in the strawberry is much like that in other plants. The growing point within the crown flattens out as it develops so that the berry and stem are flattened from a slight to a considerable extent. When fasciation starts, a whole series of effects is produced depending on the extent of fruit-bud formation and on the degree to which the plants are affected. Slightly affected plants can only be distinguished by their broad-shaped primary flowers and by berries with flattened stems at the time of flowering and fruiting. (Figure 22*A*). Though the primary berries of some varieties are normally wedge-shaped, no known variety has flattened fruit stems unless it is fasciated.

If the fasciated condition has progressed somewhat further than is indicated by a flattened stem and a wedge shape of the primary berry, the berry may be coxcomb-shaped, curled or recurved (Figures 22*A*, 23*A* and *B*), and the secondary and later berries may be much smaller than those on normal plants. The leaves are also far smaller and more erect and have petioles which are more slender than normal. For example, 10 leaves of a severely fasciated Fairfax plant averaged 3.0 square inches in area and 10 leaves of the adjacent normal Fairfax plant averaged 17.4 square inches. Figure 21*B* shows the difference in leaf size of the Eleanor Roosevelt variety. The peduncle may become from one to two inches in width (Figure 21*A*). The secondary and even some tertiary berries may be coxcomb-shaped or distorted, and their pedicels joined to the pedicel and peduncle of the primary berry. Most of the secondary and tertiary flowers do not set fruit and the clusters may be much larger than on normal plants (Figure 23*A*).

In severe cases the primary berry becomes worthless or may not develop at all. If the primary berry does not develop, usually no berries or possibly only a very few small secondary berries are produced. Such plants have masses of minute leaves. They resemble plants injured by cold and drought which have pushed out of the ground but are still

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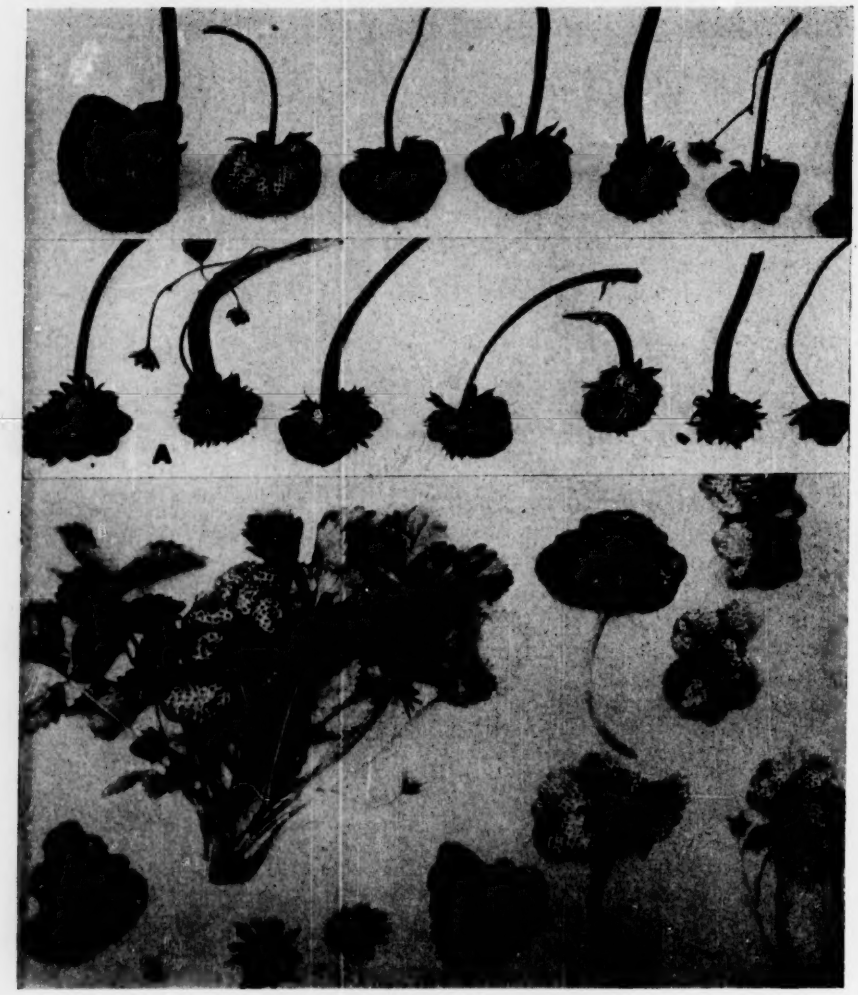


FASCIATED STEMS AND FRUITS

Figure 22

A—Fasciated pedicels and berries of the Fairfax variety—top left, fleshy fruits; top right, worthless fruits; below, all worthless abortive berries. *B*—Fasciated stems and fruits of affected strawberry plants. The extreme convolutions shown here are caused by the extent of the lateral growth of the berries. This distortion must start at a very early stage of bud differentiation when the fleshy fruit begins to outgrow the pedicel yet the fibrovascular bundles are continuous.

living. If affected plants are left for a second season the affected parts ordinarily do not produce runners and they finally die. None has been known to recover.

One, two, three, four or all crowns on a plant may be fasciated. The one or more normal crowns on partly fasciated plants may produce normal leaves, fruit and runners (Figure 23*B*).

Runner plants from mother plants that became fasciated seem more likely to become fasciated than those from mother plants that do not show fasciation. During the first season, though leaves become small, and petioles slender, these are the only evidences of fasciation. No flattened runners or roots have been observed.

Some affected plants can be distinguished in late summer and fall by their mass of small leaves. However, the condition is easier to identify when growth starts in the spring. The color of the leaves does not differ from those on normal plants; nor does the color or the taste of the fasciated berry differ from normal.

Distribution

As stated previously, fasciation is chiefly a defect of certain strawberry varieties in the Middle and South Atlantic States. It is rare in New England and New York, common in New Jersey, causes economic losses in Maryland, and is one of the limiting factors in the adaptation of varieties in the South. Mother plants of Redstar are severely affected in Maryland. Fairfax, Howard 17 (*Premier*), and Eleanor Roosevelt varieties have enough of the trait to affect their commercial value in eastern North Carolina. In test plantings there in April, 1940, all 25 mother plants of Fairfax and 15 of 23 mother plants of the Eleanor Roosevelt variety were fasciated. In breeding work many seedlings and selections are discarded both in Maryland and in North Carolina. Through a score of years, while studying the major southern and eastern varieties in hundreds of fields, the senior author has never observed the characteristic in Missionary, Blakemore, and Albritton, and has seen it in but three plants of Klondike and in only a few of Massey.

Experimental plantings have been under observation for many years at Willard, North Carolina, where many plants are seriously affected. In April, 1940, fasciated plants in varieties and selections were counted (Table I).

TABLE I. Fasciated plants of strawberry varieties and selections, April 1940, Willard, North Carolina.

Variety or selection	Plants counted number	Plants fasciated percent	Notes
Blakemore	400	0	Never found in this variety
Bellmar	†	0	Rarely found in this variety
Daybreak	400	0	
Dorsett	†	0	Has been found in this variety
Eleanor Roosevelt:			
Mother plants	100	81	
June-rooted	128	2	
August-rooted	120	0	
Fairfax:			
Mother plants	25	100	
June-rooted	100	29	
August-rooted	100	8	
Fairmore	100	0	Has been found in this variety
Klondike	400	0	Only 3 plants ever observed
Massey	400	0	
Missionary	400	0	Has not been found in this variety
NC-112	200	14	
NC-151	200	0	
NC-311	400	0	
NC-331	8	50	
NC-333	200	2	
NC-640	200	0	

*Parentage of selections in this and other tables:
NC-112—(Record lost) × Fairfax
NC-151—US-778 × Fairfax
NC-222—(Parentage record lost)
NC-302—Blakemore × Fairfax
NC-311—Blakemore × Fairfax
NC-331—US-652 × Fairfax
NC-333—US-652 × Redheart
NC-640—US-778 × Fairfax
NC-855—US-2309 × US-1008
NC-866—Blakemore × NC-302
US-652—Red Sugar × Howard 17
US-778—Missionary × Howard 17
US-1936—Blakemore × Klondike
US-1008—Howard 17 × *F. chiloensis*
US-2309—Blakemore × Klondike
†50-ft. row

Inheritance

In 1940 there were two fields of F_1 seedlings of varieties and selections at Willard, North Carolina, making it possible to obtain records on the inheritance of fasciation. One field of selfed seedlings was two years old and the other was one year old. In certain lots of the two year old seedlings, chiefly in those of selfed Fairfax and Eleanor Roosevelt varieties, many seedlings died in 1939, probably as a result of the anomaly. Therefore the percentage of affected plants probably should be greater than is given in Table II.

The selfed progeny of three varieties, Fairfax, Fairmore and Eleanor Roosevelt, and the F_2 of an unnamed selection, NC-302, showed a considerable percentage of fasciated seed-

TABLE II. F_1 and F_2 fasciated strawberry seedlings, Willard, North Carolina, April 1940*

Year grown and variety or selection	Plants counted number	Plants fasciated percent
Seedlings grown in 1938:		
Blakemore (F_1)	315	2
Blakemore (F_2)	7	0
Daybreak (F_1)	119	3
Fairfax (F_1)	160	39
Fairmore (F_1)	93	11
Eleanor Roosevelt (F_1)	80	31
Klondike (F_1)	52	0
Missionary (F_1)	117	0
Southland (F_1)	134	1
NC-302 (F_1)	13	0
NC-302 (F_2)	57	31
US-1936 (F_1)	24	4
Seedlings grown in 1939:		
NC-866 (F_1)	132	1
NC-640 (F_1)	95	0
Klondike (F_2)	312	0
Fairmore (F_1)	50	4
Massey (F_2)	208	8

*See footnote Table I for parentage of selections.

FASCIATED SEEDLING AND CROWNS

Figure 23

A—Fasciated strawberry seedling (Fairmore × NC-866). This plant has a massive fasciated peduncle or stem and the primary, secondary and most of the tertiary flowers did not set. *B*—Plant of Howard 17 (*Premier*) with leaves picked off to show its three crowns, a fasciated central crown and two lateral normal crowns.

lings. Plants of these three varieties also showed a high percentage of fasciation, particularly in the mother plants which were comparable in age with seedlings fruiting for the second year. The one year old selfed seedlings (1939 lot) showed but little of the defect.

In order to determine whether fasciation might be a mutation, we grew selfed seedlings of fasciated and non-fasciated plants of NC-302 (Blakemore × Fairfax), but no more fasciated seedlings appeared in the fasciated line than in the normal line.

Also available for study were several hundred seedlings from varietal crosses fruiting for the second time as well as several thousand seedlings from varietal crosses fruiting for the first time from which records of the inheritance of fasciation were obtained (Table III).

When these seedlings had been in the field for one or two years and were observed in 1940, the majority of them did not show fasciation. With some understanding of the inheritance of this anomaly, and of the conditions under which it is expressed, it seems possible to avoid serious losses in seedlings and to breed varieties relatively free from this undesirable characteristic.

Relation of Faciation to Photoperiodism

In the fall of 1951 fasciated plants of eight varieties were observed in a photoperiod experiment at Beltsville, Maryland.* Except for three plants in each lot of the Howard 17 (*Premier*), which were set May 18, the plants were set in boxes May 9 (Figure 24). The number of plants in each test was 20 for Missionary, Klondike, Tennessee Beauty, and Howard 17, and 10 for Blakemore, Massey, Mastodon, and Redstar. One plant of Klondike in the 11-hour trial died. Duplicate lots were subjected to eight different photoperiod experiments. Five of these consisted of single alternations of light and dark each 24 hours, the light durations being 8, 11, 14, 17, and 20 hours. Plants given the other three trials received two light periods during each 24 hours, the first one was of 11 hours duration. The second was a dark-period interruption of one third, one or three hour duration near the middle of this period. The 8- and 11-hour lots received natural light only. To complete the scheduled tests all other lots received 11 hours of natural light and artificial light of 20 to 40-foot-candle intensity for incandescent-filament lamps. These eight photoperiod experiments were continued for nearly six months, until October 31, when records were made of plants showing fasciation (Table IV).

No fasciation was found in Missionary, Blakemore, and Massey and it was observed in only one plant of Tennessee Beauty, in the eight-hour photoperiod experiment. Plants of Klondike and Mastodon given the eight- and 11-hour trials showed some fasciation but those given longer photoperiods did not. Howard 17 (*Premier*) and Redstar showed fasciation in all or nearly all experiments, Redstar being affected more often than Howard 17.

Discussion and Summary

It is evident that a tendency to fasciate is inherited in certain lines of strawberries. Fairfax is subject to fasciation and a large proportion of its seedlings show it. Some varieties derived in part from Fairfax, such as Eleanor Roosevelt, Sparkle, and Redstar, also

*Borthwick, H. A., and M. W. Parker. Light in relation to flowering and vegetative development. Report of the 13th International Hort. Cong. of the Royal Hort. Soc., London. Sept. 8-15, 1952. Pp. 801-810.

show this defect, and seedlings from these varieties may inherit a tendency toward fasciation. In North Carolina the older plants may show fasciation when young plants do not. In a planting at Willard, North Carolina, all the mother plants of Fairfax were fasciated, but only 29 percent of the June-rooted plants and only eight percent of the August-rooted plants were fasciated by the following April (Table I).

The photoperiod tests show that fasciation is increased in susceptible varieties by short, daily light periods. None of the photoperiods tested caused fasciation in Missionary, Blakemore and Massey. It may be that no short photoperiods long enough to permit plant growth is effective in causing fasciation in the first two varieties. Inasmuch as fasciation has been observed in Massey in the field, shorter photoperiods might have been effective with this variety. The response of other varieties varies with the duration of the period of light and darkness. Even a 20-hour photoperiod under the conditions of the experiment was not effective in stopping all fasciation in Redstar. However, we have not observed fasciation in Redstar in New England where photoperiods of about 16 hours occur in midsummer.

Fasciation apparently is initiated mostly in the fall when the days shorten, just at the time when fruit buds develop. There is no evidence, however, that the two phenomena are necessarily related. Fasciation is always much worse in southern than in northern states. It is hardly known in the Fairfax variety in regions as far north as New York and New England; it is so serious in the south that it

PHOTOPERIOD EXPERIMENT

Figure 24

Strawberry trays on flat cars for different photoperiods. The house in the rear is used for short photoperiod experiments with various plants.

becomes a limiting factor in the growing of this variety. The somewhat shorter photoperiods throughout the growing season in Maryland, as compared with New York, have a major effect in producing fasciation on such varieties as Redstar and Fairfax, and Maryland is about the southern limit for their commercial production. Howard 17 (*Premier*) produces well a little farther south than Redstar and Fairfax, but fasciates too much for good production in North Carolina. It is evident that varieties that fasciate are not adapted to southern States.

Though a short photoperiod is the major factor in producing fasciation in sensitive varieties, growth conditions and age of plant also must affect fasciation. Thus, the mother plants of both Eleanor Roosevelt and Fairfax (Table I) were all or nearly all fasciated, while the June- and August-rooted plants showed far less fasciation. Older plants are

TABLE III. Fasciated seedlings in the 1938 and 1939 progenies of strawberry crosses, Willard, North Carolina, 1940*

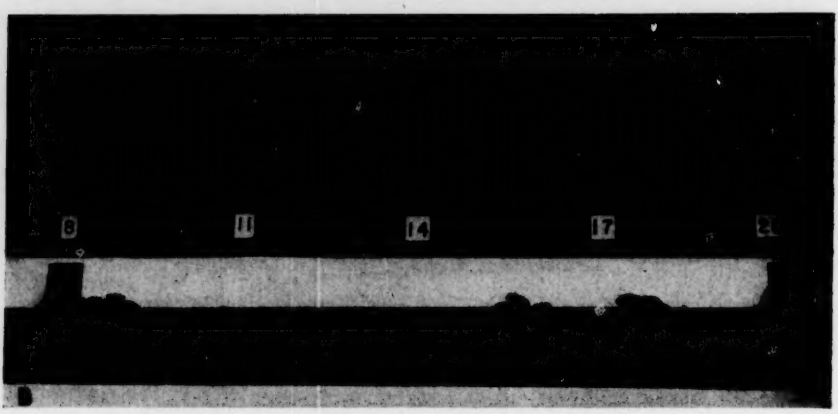
Year grown and cross	Plants counted number	Plants† fasciated percent
Seedlings grown in 1938:		
NC-222 × Fairmore	107	5
NC-222 × Fairfax	85	29
Blakemore × Fairfax	226	13
Fairmore × Daybreak	115	1
Seedlings grown in 1939:		
Blakemore × Massey	282	5
Blakemore × NC-640	194	3
Blakemore × Dresden	109	6
Blakemore × Missionary	153	2
Catskill × Blakemore	292	5
Catskill × Fairmore	383	4
Catskill × Massey	337	2
Catskill × NC-866	310	1
Daybreak × NC-855	50	0
Dorsett × NC-866	331	2
Fairmore × Dresden	86	9
Fairmore × NC-640	657	3
Fairmore × NC-866	89	7
Massey × Fairmore	334	4
Massey × NC-640	254	4
Missionary × Blakemore	47	0
Rockhill × NC-855	128	0
NC-640 × Massey	191	3
NC-640 × Redheart	283	1
NC-855 × Daybreak	157	4

*See footnote Table I for parentage of selections.
†Includes some seedlings originally listed as doubtful but later showing fasciation.

TABLE IV. Fasciation in eight strawberry varieties subjected to various photoperiods for about six months, October 31, 1951*

Variety	Percent of plants fasciated under indicated photoperiods							
	8 hours	11 hours	14 hours	17 hours	20 hours	11+⅜ hours	11+1 hours	11+3 hours
Missionary	0	0	0	0	0	0	0	0
Blakemore	0	0	0	0	0	0	0	0
Massey	0	0	0	0	0	0	0	0
Tennessee Beauty	5	0	0	0	0	0	0	0
Klondike	25	21	0	0	0	0	0	0
Mastodon	20	20	0	0	0	0	0	0
Howard 17 (*Premier*)	95	95	95	5	0	95	65	5
Redstar	100	100	100	90	20	100	100	80

*Twenty plants per lot for Missionary, Tennessee Beauty, Klondike (one plant in 11-hr. experiment died) and Howard 17; 10 plants per lot of others.



RESULTS OF THE PHOTOPERIOD EXPERIMENT

Figure 25

A—Representative plants grown under five photoperiods—8, 11, 14, 17 and 20 hours. These plants were potted from trays. Ninety-five percent of the plants under 8-, 11-, and 14-hour photoperiods were fasciated. Five percent of those under 17 hours, and none under 20-hour photoperiod were fasciated. *B*—A tray of Howard 17 (*Premier*) grown under an eight-hour photoperiod.

always more subject to the defect than younger ones. It would seem that the long duration of plant growth in southern areas under relatively short photoperiods initiates fasciation in such varieties as Howard 17 and Redstar (Table IV). In northern areas plant growth occurs for a relatively short time after September when daily light periods are short.

Observation also indicates that fasciation is much more serious in some seasons than in others. When growing conditions in the fall continue later than usual, fasciation the following season is much more serious. Thus, the Sparkle variety which usually is not too badly affected, fasciated seriously in New Jersey after the warm fall of 1952. This, however, would be expected, for fasciation is more common when the days are as short as 11 hours.

(Received February 2, 1954)

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